THE BULLETIN OF
Mathematical
BIOPHYSICS

THE UNIVERSITY OF CHICAGO PRESS · CHICAGO · ILLINOIS

VOLUME 10
1948

PUBLISHED, MARCH, JUNE, SEPTEMBER AND DECEMBER, 1948
PRINTED BY THE DENTAN PRINTING CO., COLORADO SPRINGS, COLO.

CIRCULATE

THE BULLETIN OF Mathematical BIOPHYSICS

MARCH 1948

MATHEMATICAL BIOPHYSICS OF SOME NEURAL NETS—*J. B. Roberts* 1

ON THE LOCOMOTION OF MAMMALS — *N. Rashevsky* - - - 11

SOME MECHANICAL FACTORS IN THE DYNAMICS OF THE THIN-WALLED, SPHERICAL VISCUS — *Daniel A. Brody and J. P. Quigley* - - - - - - - - - - - - - - - 25

THE MECHANISM FOR OPTIC NERVE CONDUCTION AND FORM PERCEPTION: I. — *J. T. Culbertson* - - - - - - - - - 31

A STATISTICAL APPROACH TO THE THEORY OF THE CENTRAL NERVOUS SYSTEM — *Alfonso Shimbel and Anatol Rapoport* - - 41

UNIVERSITY OF HAWAII
APR 20 1948
LIBRARY

THE UNIVERSITY OF CHICAGO PRESS · CHICAGO · ILLINOIS
VOLUME 10 · · · · · NUMBER 1

THE BULLETIN OF MATHEMATICAL BIOPHYSICS

EDITED BY N. RASHEVSKY

The Bulletin is devoted to publications of research in Mathematical Biophysics, as described on the inside back cover.

THE BULLETIN is published by the University of Chicago at the University of Chicago Press, 5750 Ellis Avenue, Chicago, Illinois, quarterly, in March, June, September, December. ¶The subscription price is $4.00 per year, the price of single copies is $1.25. Orders for service of less than a full year will be charged at the single-copy rate. ¶Patrons are requested to make all remittances payable to The University of Chicago Press in postal or express money orders or bank drafts.

THE FOLLOWING are authorized agents:

For the British Empire, except North America, India, and Australasia: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices of yearly subscriptions and of single copies may be had on application.

CLAIMS FOR MISSING NUMBERS should be made within the month following the regular month of publication. The publishers expect to supply missing numbers free only when losses have been sustained in transit, and when the reserve stock will permit.

BUSINESS CORRESPONDENCE should be addressed to The University of Chicago Press, Chicago, Ill.

COMMUNICATIONS FOR THE EDITOR and manuscripts should be addressed to N. Rashevsky, Editorial Office of the Bulletin of Mathematical Biophysics, 5822 Drexel Avenue, Chicago, Ill.

IMPORTANT ANNOUNCEMENT

The increase in the output of papers in the field of mathematical biophysics makes it difficult to insure prompt publication without an increase in the size of the journal. Therefore, the Bulletin of Mathematical Biophysics inaugurates the following service:

Upon acceptance of a paper, the Editor will, if necessary, ask the author to shorten the paper to an extent dictated by the requirements of a reasonably prompt publication. The shortening should in no case reduce the paper to a mere abstract. Such a shortened paper will be published within six months or less.

The unabbreviated original manuscript will be kept on file at the editorial office. Any person desiring to avail himself of the complete manuscript may obtain promptly a microfilm copy of the latter, at the cost of 2¢ per page plus a carrying charge of 25¢ and postage, by applying to the Editorial Office, 5822 Drexel Avenue, Chicago, Illinois.

All papers in the Bulletin which have been thus shortened will be marked at the end by the symbol MF followed by a figure indicating the number of double-spaced typewritten pages of the unabbreviated manuscript.

PRINTED BY THE DENTAN PRINTING COMPANY . . . COLORADO SPRINGS, COLORADO

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 10, 1948

MATHEMATICAL BIOPHYSICS OF SOME NEURAL NETS

J. B. ROBERTS
THE UNIVERSITY OF CHICAGO

Methods are considered for constructing neural nets of the McCulloch-Pitts type giving arbitrary time delays between stimuli and their responses. By introducing cycles of neurons, the problem is treated from the standpoint of economizing on the number of neurons required. A generalization is effected that will realize any unique temporal response pattern from a unique stimulus.

Time Delay Circuits. The "microscopic picture" of neural nets (McCulloch and Pitts, 1943) considers individual neurons and synapses. Time is regarded as "quantized" rather than continuous, and only spatial and not temporal addition of impulses at synapses is provided for.

The construction of a neural net such that any desired finite time delay, of N units between the action of a stimulus S and the action of a response R, is incorporated in the net, can be made very simply by inserting a chain of $N—1$ synapses between the neuron stimulated and that responding. Clearly, we can make the delay as long as we desire.

However, we wish to devise a net that will give a time delay of, say, N time units using less than N synapses. Such an economy can be realized in neural nets involving cycles of neurons, i.e., sets of neurons $b_1, \cdots, b_r$ connected in "series" such that b_r is connected to b_1. Thus a cycle is a repeating system.

By using such cycles we can devise, with relatively few neurons, nets with time delays of any finite length. In the example shown in Figure 1, we have two cycles, of five synapses and of seven synapses respectively. The response R will occur at 36 time units after S. The net represented in Figure 1 gives this time delay of 36 with the use of only 13 synapses. The dotted lines in the Figure represent connec-

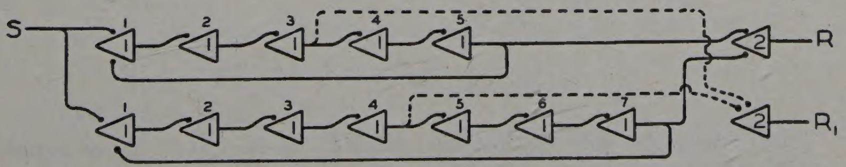

FIGURE 1

tions of other neurons to response R_1, which occurs at 19 time units after S. In general, this net will give a response for any time delay from 2 to 36. Any such response for this net will be repeated at intervals of 35 time units. Note that the period P of the net is equal to the product of the numbers of synapses in the individual cycles and that the "range" of time delays this circuit can give is from 2 to $P + 1$.

We will now discuss the specific construction of a net for some particular time delay O_T. We will represent the number of cycles by r and the number of synapses in each cycle by $N_i \, (i = 1, \cdots, r)$.

In the construction of the nets under consideration we will use the following two notions:

(1) The *effective factors* (*EF*'s) of a net (defined for nets of the type shown in Figure 1 only). For these nets there is one *EF* for each cycle, and the *EF* corresponding to any particular cycle has a value equal to the number of synapses in that cycle.

(2) The highest common normal factor of a set of r numbers ($HCNF_r$). This is defined by the following relation:

$$HCNF_r = \frac{\prod_{i=1}^{r} N_i}{LCM(N_1, \cdots, N_r)}, \tag{1}$$

where LCM is the "lowest common multiple."

It can be verified that

$$LCM(N_1, \cdots, N_r) = P(N_1, \cdots, N_r), \tag{2}$$

where P is the period of the net. For a circuit similar to that of Figure 1 we know that the range is from 2 to $P + 1$ and therefore also from 2 to $LCM(N_1, \cdots, N_r) + 1$. So, given an O_T value, we can state the following. If

$$LCM(N_1, \cdots, N_r) + 1 \geqq O_T, \tag{3}$$

then the net with cycles $N_1, \cdots, N_r$ will realize a time delay of O_T time units.

Combining equations (1) and (3) we get

$$\frac{\prod_{i=1}^{r} N_i}{HCNF_r} \geqq O_T - 1. \tag{4}$$

It will now be shown that the $HCNF_r$ of $N_1, \cdots, N_r$ is equal to the HCF (highest common factor) of the r products

$$\frac{\overset{r}{\underset{i=1}{\Pi}} N_r}{N_j}; \ (j = 1, \cdots, r).$$

Breaking $N_1, \cdots, N_r$ into prime power factors, we get

$$\begin{aligned} N_1 &= a^{\alpha_1} \cdot b^{\beta_1} \cdot c^{\gamma_1} \cdots \\ N_2 &= a^{\alpha_2} \cdot b^{\beta_2} \cdot c^{\gamma_2} \cdots \\ &\cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot \\ N_r &= a^{\alpha_r} \cdot b^{\beta_r} \cdot c^{\gamma_r} \cdots . \end{aligned} \tag{5}$$

Call $\alpha_{\max}, \beta_{\max}, \gamma_{\max}, \cdots$, the maximum $\alpha_i, \beta_i, \gamma_i, \cdots$, present in the array (5). Then

$$HCF\left(\frac{\overset{r}{\underset{i=1}{\Pi}} N_r}{N_j}\right) = a^{\Sigma\alpha_i - \alpha_{\max}} \cdot b^{\Sigma\beta_i - \beta_{\max}} \cdot c^{\Sigma\gamma_i - \gamma_{\max}} \cdots . \tag{6}$$

Also from (1) and (5) we have

$$\begin{aligned} HCNF_r &= a^{\Sigma\alpha_i - \alpha_{\max}} \cdot b^{\Sigma\beta_i - \beta_{\max}} \cdot c^{\Sigma\gamma_i - \gamma_{\max}} \cdots \\ &= \frac{\overset{r}{\underset{i=1}{\Pi}} N_r}{LCM(N_1, \cdots, N_r)}, \end{aligned} \tag{7}$$

which was to be shown. We will use the above result for the computing of the LCM, which in many cases can be done more readily by breaking the numbers down into their prime factors and choosing the proper ones for the LCM.

From relation (4) we see that there are an indefinite number of sets of EF's for any finite O_T. This suggests that one can find a "best set" (or set of best sets) of EF's in the sense of the one giving the required range and having the least sum. This problem is not solved here. It is true that a best set for a given range will have the property $(N_i, N_j) = 1$; $(i \neq j)$, but this condition is not sufficient. If $N_1, \cdots, N_r$ are relatively prime in pairs, then we have $HCNF_r = 1$. If only one pair, say, $(N_i, N_j) = d$, then the $HCNF_r > 1$. (In this case, $HCNF_r = d$.)

As an example find the range of the set of EF's: $N_1 = 2$, $N_2 = 4$, $N_3 = 9$, $N_4 = 6$. We have

$$\begin{aligned} &HCNF_4(2, 4, 9, 6) \\ &= \frac{2 \cdot 4 \cdot 9 \cdot 6}{HCF(2 \cdot 4 \cdot 9, 2 \cdot 4 \cdot 6, 2 \cdot 9 \cdot 6, 4 \cdot 9 \cdot 6)} = \frac{2 \cdot 4 \cdot 9 \cdot 6}{12} = 36. \end{aligned}$$

From (4) we have $O_T \leqq 37$. The range is therefore from 2 to 37. In this case the threshold of the last synapse before the response R would be 4 (synapse q in Figure 1). In general, the thresholds of such synapses (q-synapses) will be equal to the number of cycles r.

Given a circuit with a range of 2 to $\left(\frac{N_1, \cdots, N_r}{HCNF_r} + 1\right)$, we wish to know which synapses in the individual cycles should be connected to a single q-synapse in order to give a particular time delay. To do this, we set up the following ordering. Construct a table with r columns and with $LCM(N_1, \cdots, N_r)$ rows. In the first column of this table write downward the numbers $1, 2, \cdots, N_1$, repeating until column is filled. Do the same with the numbers $1, 2, \cdots, N_2$ in column two, etc. Table I is an example of the case for three EF's having the values $N_1 = 2$, $N_2 = 3$, $N_3 = 6$. We label the columns $d_1, \cdots, d_r$ and the rows from 2 to $LCM + 1$. The last row of Table I consists of N_1, N_2, N_3. The last row of any table constructed in this manner will consist of the entries $N_1, \cdots, N_r$. The number of repetitions of $N_1, \cdots, N_k$ in column k of the table is equal to LCM/N_k. Each row number corresponds to one O_T value. Thus the range of the row numbers corresponds to the range of the circuit that the table represents. Therefore, for every O_T value in the range, there corresponds a set $d_1, \cdots, d_r$. By the construction of our table, we see that the sets $(d_1, \cdots, d_3)_T$, $T = 2, \cdots, 7$, indicate the synapse numbers in cycles $1, \cdots, 3$ which realize the O_T corresponding to each set. It follows immediately that the sets $(d_1, \cdots, d_r)_T$ in any such table of r cycles are all distinct.

TABLE I

	d_1	d_2	d_3
2	1	1	1
3	2	2	2
4	1	3	3
5	2	1	4
6	1	2	5
7	2	3	6

We will call the set $d_1, \cdots, d_r$ for a particular O_T the "description number" (DN) for that O_T.

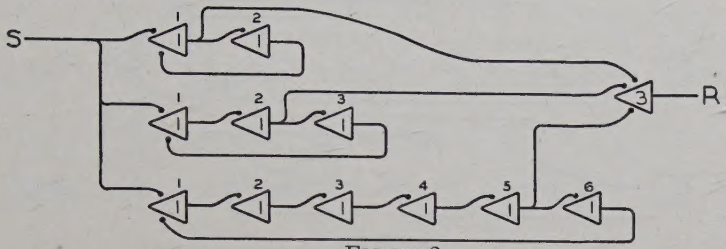

FIGURE 2

In Figure 2 we have the circuit corresponding to Table I. From the Table we can choose a row number (equal to a desired O_T between 2 and 7), say 6, and find its set of d's to be $d_1 = 1$, $d_2 = 2$, $d_3 = 5$. Thus d_i indicates which synapse in cycle i is connected to q for some particular O_T.

When the N_i's are not relatively prime in pairs, there will always be certain sets $(d_1, \cdots, d_r)$ that will not appear in the table of DN's for the circuit. These DN's not appearing correspond to sets of neurons that will never fire together.

The number of synapses used for a particular O_T is equal to $(N_1 + N_2 + \cdots + N_r + 1)$ while the range of delays is from 2 to $LCM + 1$.

Generalization of the Construction. Examining Table I, we see a certain regularity. For example, if we look at the row labeled T we note

$$\begin{aligned} T &\equiv d_1 + 1 \bmod N_1\,, \\ T &\equiv d_2 + 1 \bmod N_2\,, \\ T &\equiv d_3 + 1 \bmod N_3\,. \end{aligned}$$

For any table constructed in the manner of Table I, we have the following set of relations holding (where ${}_T d_i$ stands for the entry in the T-th row and the i-th column):

$$(T)\,[2 \text{ to } LCM + 1]\,(i)\,[r]\,[T \equiv {}_T d_i + 1 \pmod{N_i}]\,. \qquad (8)$$

This congruence (8) enables us to construct a circuit giving a desired delay of, say, O_T by simply solving the proper congruences.

The following method of constructing a circuit gives a unique temporal response pattern for the action of R. If the response R is to occur at the times $\tau_1, \cdots, \tau_p$, then we can construct a circuit giving responses $R_1, R_2, \cdots, R_p$ with the time delays of $O_{T_1} = \tau_1 - 1, \cdots, O_{T_p} = \tau_p - 1$ (where S acts at $\tau = 0$), and then connect each of these responses with the response R that is to occur once for each of these.

Where we have a sequence of impulses all causing the same response R, then we have one extra delay introduced in the circuit over

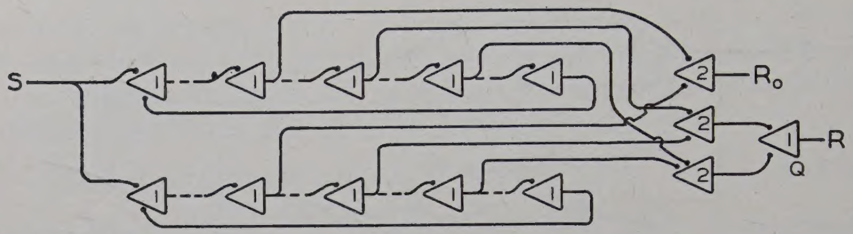

FIGURE 3

that for the responses R_i (see Figure 3). This extra delay is introduced by the synapse labeled Q. With O_T still indicating the time delay between the stimulus S and the final response, we see that we can use all the equations given previously if we correct for the extra time unit. This can be done by using in them the value of O_T' is given by

$$O_T' = O_T - 1 . \tag{9}$$

The range for a sequence is from 3 to $LCM(N_1, \cdots, N_r) + 2$.

From congruence (8) we have Table II, where the O_{T_i} are the delays of action of R. With Table II we can find DN's for any sequence of time delays, provided a suitable set of EF's is chosen. Any set of EF's found for the largest time delay will suffice.

TABLE II

	d_1 $(i=1)$	d_2 $(i=2)$	d_3 $(i=3)$	d_r $(i=r)$
$O_{T_i} \equiv 0 \pmod{N_i}$	$N_1 - 1$	$N_2 - 1$	$N_3 - 1$	$N_r - 1$
$O_{T_i} \equiv 1 \pmod{N_i}$	N_1	N_2	N_3	N_r
$O_{T_i} \equiv 2 \pmod{N_i}$	1	1	1	1
$O_{T_i} \equiv 3 \pmod{N_i}$	2	2	2	2
$O_{T_i}' \equiv 4 \pmod{N_i}$	3	3	3	3
$O_{T_i} \equiv N_1 - 1 \pmod{N_i}$	$N_1 - 2$	. . . .	. . . .	. . . .
$O_{T_i} \equiv N_2 - 1 \pmod{N_i}$		$N_2 - 2$	. . . .	. . . .
$O_{T_i} \equiv N_3 - 1 \pmod{N_i}$			$N_3 - 2$	. . . .
$O_{T_i} \equiv N_r - 1 \pmod{N_i}$				$N_r - 2$

As an example, find a circuit giving R at times giving delays of $O_{T_1} = 4$, $O_{T_2} = 6$, $O_{T_3} = 9$, $O_{T_4} = 13$, after action of S. The largest O_T is $O_{T_4} = 13$. From (9) we have $O_{T_4}' = 13 - 1 = 12$, so that if $N_1 = 3$, $N_2 = 4$, then from (4) we have $\frac{N_1 \cdot N_2}{HCNF_2} = \frac{3 \cdot 4}{1} \geqq O_{T_4}' - 1 = 12$. Using Table II we obtain:

	d_1 $(i=1)$	d_2 $(i=2)$
$O_{T_i} \equiv 0 \pmod{N_i}$	2	3
$O_{T_i} \equiv 1 \pmod{N_i}$	3	4
$O_{T_i} \equiv 2 \pmod{N_i}$	1	1
$O_{T_i} \equiv 3 \pmod{N_i}$		2

With this we can obtain next:

	d_1	d_2
$3 = O_{T_1}' \equiv 0 \pmod{3}$	2	
$3 = O_{T_1}' \equiv 3 \pmod{4}$		2
$5 = O_{T_2}' \equiv 2 \pmod{3}$	1	
$5 = O_{T_2}' \equiv 1 \pmod{4}$		4
$8 = O_{T_3}' \equiv 2 \pmod{3}$	1	
$8 = O_{T_3}' \equiv 0 \pmod{4}$		3
$12 = O_{T_4}' \equiv 0 \pmod{3}$	2	
$12 = O_{T_4}' \equiv 0 \pmod{4}$		3

This final table gives the DN's of 2,2; 1,4; 1,3; 2,3 for $O_{T_1} = 3$, $O_{T_2} = 5$, $O_{T_3} = 8$, $O_{T_4} = 12$.

The circuit is given in Figure 4. This can be checked by the method of activity matrices (Landahl and Runge, 1946).

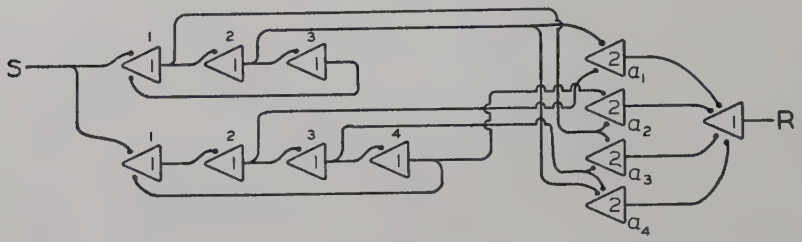

FIGURE 4

Now if we wish to write Table II more compactly, at the same time allowing us to insert n—2 synapses between S and the cycles, we can do so with Table III. The χ_i's and q_i's in Table III are defined

TABLE III

χ_1	d_i
0	$N_i - q + 1$
1	$N_i - q + 2$
2	$N_i - q + 3$
....	....
$n - 1$	N_i
n	1
$n + 1$	2
....	....
$N_i - 1$	$N_i - q$

by the following congruences, where the O_T's are the time delays and the N_i's, the EF's. (In any row of the table, if $N_i - q + p > N_i$, then it is reduced modulo N_i.) We have

$$n \equiv q_i \pmod{N_i}, \tag{10}$$

$$O_T \equiv \chi_i \pmod{N_i}. \tag{11}$$

The range for this case is from $n + 1$ to $LCM + n$. Instead of condition (4), the following holds:

$$LCM(N_1, \cdots, N_r) \geqq O'_{T_{\max}} - O'_{T_{\min}}, \tag{12}$$

since only the spread of the time delays, so to speak, determines the *EF*'s.

We now consider as an example the circuit given in Figure 4 and make the proper connections to give R at time delays after S of $O_{T_1} = 3$, $O_{T_2} = 6$, $O_{T_3} = 8$, $O_{T_4} = 9$. We see that $N_1 = 3$, $N_2 = 4$, $N_3 = 6$. With these and the O_T values, we get from congruences (10) and (11) and Table II the following table:

	O_T'	χ_1	χ_2	χ_3	d_1	d_2	d_3
a_1	2	2	2	2	1	1	1
a_2	5	2	1	5	1	4	4
a_3	7	1	3	1	3	2	6
a_4	8	2	0	2	1	3	1

From this we see the *DN*'s are 1,1,1; 1,4,4; 3,2,6; 1,3,1. The circuit is similar to that of Figure 4. Again the circuit can be checked using the method of H. D. Landahl and R. Runge mentioned previously.

For another example, find a circuit for R to act after a delay of $O_{T_1} = 11$, $O_{T_2} = 14$, $O_{T_3} = 16$, $O_{T_4} = 17$, with $n = 10$. From congruence (10) we have

$$\begin{aligned} 10 &\equiv 1 \pmod{3}, & q_1 &= 1; \\ 10 &\equiv 2 \pmod{4}, & q_2 &= 2; \\ 10 &\equiv 4 \pmod{6}, & q_3 &= 4. \end{aligned}$$

Also, we have from congruence (11) the χ_i values for Table III. And from relation (12) we see that in this example the *EF*'s, $N_1 = 3$, $N_2 = 4$, $N_3 = 6$, will suffice, since $\frac{3 \cdot 4 \cdot 6}{6} = 12 \geqq O_{T_4}' - O_{T_1}' = 16 -$

$10 = 6$. This gives us the table:

O_{T_i}'	χ_1	χ_2	χ_3	d_1	d_2	d_3
10	1	2	4	1	1	1
13	1	1	1	1	4	4
15	0	3	3	3	2	6
16	1	0	4	1	3	1

Therefore the *DN*'s needed are 1,1,1; 1,4,4; 3,2,6; 1,3,1. These are the same as in the previous example, as they should be, since we have merely inserted 8 time units between S and the cycles, while keeping the differences of the O_T values constant. We would not have obtained the same had we changed the differences of the O_T's.

The author wishes to express his thanks to Dr. A. Rapoport for a critical reading of this paper.

This work was aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

LITERATURE

Landahl, H. D. and R. Runge. 1946. "Outline of a Matrix Calculus for Neural Nets." *Bull. Math. Biophysics*, 8, 75–81.

McCulloch, W. S. and W. Pitts. 1943. "A Logical Calculus of the Ideas Immanent in Nervous Activity." *Bull. Math. Biophysics*, 5, 115-133.

Rashevsky, N. 1945. "A Reinterpretation of the Mathematical Biophysics of the Central Nervous System in the Light of Neuro-physiological Findings." *Bull. Math. Biophysics*, 7, 151–160.

Rashevsky, N. 1945. "Some Remarks on the Boolean Algebra of Nervous Nets in Mathematical Biophysics." *Bull. Math. Biophysics*, 7, 203–211.

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 10, 1948

ON THE LOCOMOTION OF MAMMALS

N. RASHEVSKY
THE UNIVERSITY OF CHICAGO

By considering the general energy balance between the energy of muscular contraction in the extremities, kinetic energy imparted to the animal and the energy lost in the lifting of the center of gravity and in the possible muscular viscosity, an expression is derived for the speed of an animal in terms of the constants which determine its shape and structure. The relation discussed previously, namely, that the speed is proportional to the square root of the length of the extremities, turns out to be only a first rough approximation in a rather special case. Reasons are given for the number of joints actually observed in animal extremities.

In a previous paper (Rashevsky, 1944b) we discussed the dynamics of locomotion of "quadrupeds." It is better to refer more specifically to "quadruped mammals" since, technically, such animals as lizards are also quadrupeds though the dynamics of their locomotion are very different. On the other hand, the same considerations as discussed in *loc. cit.* may apply to the leaping of a frog or even of a grasshopper.

In that paper it was shown that velocities of locomotion usually observed in most mammals could not be obtained with rigid extremities simply swinging to and fro, and that a flexible extremity having at least one joint is necessary to obtain such velocities. The extremities act as a sort of "spring" which repels the animal from the ground. It was also pointed out that as a first approximation the action of only one pair of extremities, the rear ones, is essential, and that the existence of four pairs was probably determined by other considerations than speed.

By very crude semi-kinematical considerations we derived a relation between the length of the extremity and maximum speed of the animal, and found that the latter should vary approximately as the square root of the length of the extremities. Quantitative data on the speed of animals are, to put it mildly, very scarce. Whatever data are available seem to bear out roughly the derived relation.

The derivation of the above relation being in many respects rather unsatisfactory, it is the purpose of this paper to improve on the development of the theory. An even remotely exact theory is at present impossible because the equations of motion of a chain of linked levers (Fisher, 1906; Rashevsky, 1944c), as exemplified in an extremity of an animal, are of such a nature that the mathematician can only stare at them helplessly. Adequate methods of approximation have not as yet been developed. We shall attempt to circumvent the difficulty by consideration of an over-all energy balance. We thus shall find a more complex relation between the speed of an animal and its size and shape, a relation of which the one previously derived may be considered as a first rough approximation. We shall also throw some light on the actual number of joints in an animal extremity, a question important in the theory of organic form.

The mathematical treatment used in this paper will of necessity be very crude. We shall be more interested in orders of magnitude than in actual values, and in the general type of functional relations than in the absolute values of the coefficients of the functions involved. This must be kept in mind.

Running is essentially a series of consecutive jumps. During each jump the animal is for a while completely without contact with the ground, its center of gravity describing a parabola during the "flight" phase. If at the end of each jump the total kinetic energy of the animal were completely lost, then the mechanism of running would be identical with the mechanism of jumping. Actually only a fraction of the total kinetic energy is lost at the end of each "flight" phase. Therefore the theory of continuous running is somewhat different from the theory of jumping. We shall first consider the latter.

It is interesting to note that if the extremity were considered as a spring of original length l, contracted to a constant traction αe, and exercising a constant force F, then, neglecting its mass, we would have the following relations.

The total work done on expansion would be

$$F(l-\alpha l)=Fl(1-\alpha). \tag{1}$$

Let M denote the mass of the body and v its velocity in the direction of expansion, that is, forming an angle ϕ with the vertical. Let g be the gravity acceleration. Expression (1) must be equal to the sum of the imparted kinetic energy $\frac{1}{2}Mv^2$ and the work done in lifting the center of gravity of the body by the amount $Mg(1-\alpha)l\cos\phi$. Hence,

$$F(1-\alpha)l=\tfrac{1}{2}Mv^2=Mg(1-\alpha)l\cos\phi. \tag{2}$$

Remembering that the horizontal component v_h of v is equal to $v_h=v\sin\phi$, we find from equation (2),

$$v_h=\sqrt{\frac{2l(1-\alpha)(F-Mg\cos\phi)}{M}}\sin\phi; \tag{3}$$

that is, $v_h \propto \sqrt{l}$.

If, as corresponds better to a real spring, the force F is equal to

$$F = \frac{1}{E}\frac{l(1-\alpha)}{l} = \frac{1-\alpha}{E}, \tag{4}$$

where E is the modulus of elasticity, then, putting $(1-\alpha)l = x$, $-l d\alpha = dx$, we have for the work done by the spring,

$$\begin{aligned}\int_{(1-\alpha)l}^{0} F dx &= \frac{l}{E}\int_{\alpha}^{1}(1-\alpha)\,d\alpha \\ &= \frac{l}{E}\left[(1-\alpha) - \tfrac{1}{2}(1-\alpha^2)\right].\end{aligned} \tag{5}$$

This must be equal to $\frac{1}{2}Mv^2 + Mg(1-\alpha)\cos\phi$. Hence, again, we find that $v \propto \sqrt{l}$.

Actually the extremity is a system of linked levers. We shall assume for simplicity that the thickness of the bony core of the extremity is the same in all links, assuming the bones to be cylindrical. Let their thickness be $2b$.

The quantity b is approximately equal to the lever arm of the muscular force F which produces a torque bF in the joint. Again for simplicity, assume that the folding and extension of the extremity is complete; that is, that relative rotation of a link with respect to an adjacent one is π. Then the contraction of a muscle which produces such a relative contraction will be of the order of πb. Let the extremity consist of n *equal* links, each of length l/n. We shall number both links and joints from top down. Thus the contraction of the i-th muscle acts on the i-th joint. Altogether, $(n-1)$ muscles must contract in order to rotate the joints relative to each other. Moreover, a muscle must contract to rotate the upper joint with respect to the trunk of the animal. Hence the total number of muscles involved is n.

We shall oversimplify our picture by considering the case where each link has only one flexor and one extensor muscle. Actually, the muscle which rotates the upper link with respect to the trunk is located alongside the upper link. We shall, however, consider the purely fictitious case where it is located in the trunk. In the further development of the theory a more realistic approach will have to be used. The present departure from the real situation is justified, however, since we are at first interested primarily in some crude general relations which are not likely to depend much on the details of the structure. The assumption of equal links is in itself an abstraction. As in the early development of any theory, such abstractions are unavoidable.

Assuming the muscular force F to be constant, the total work done in extending the extremity completely from a completely folded configuration is

$$nFb\pi\,. \tag{6}$$

Very roughly, the force F may be set as proportional to the cross-section s_1^2 of the extensor muscle (Rashevsky, 1944b), where s_1 is the average thickness of the extensor muscle. Hence, denoting by f a factor of proportionality, we have

$$F = fs_1^2\,. \tag{7}$$

Since the relative contraction of any muscle does not exceed a fixed value, which is at most about 30% and is usually much less, therefore, in order to produce a contraction $b\pi$, the muscle must have a certain minimal length L. Denoting by m another factor of proportionality, we thus have $L = mb\pi$, or

$$b = \frac{L}{m\pi} = \varepsilon L\,; \quad \varepsilon = \frac{1}{m\pi}. \tag{8}$$

We have $\varepsilon\pi < 0.3$ and probably

$$\varepsilon\pi \sim 0.1\,. \tag{9}$$

Since $L = l/n$, therefore

$$b = \varepsilon l/n\,. \tag{10}$$

Hence the total work done during the extension is, by virtue of equations (6), (7), and (10),

$$W = \pi f s_1^2 \varepsilon l\,. \tag{11}$$

Denoting now by M the total mass of the animal, we find that this work is equal to the sum of $\frac{1}{2}Mv^2$ of the kinetic energy of rotation of the links of the extremity, of the work in raising the center of gravity, and of the viscous work in muscles (A. V. Hill, 1927), which we shall consider for generality. If I denotes the moment of inertia of a link having the axis passing through its center of gravity, and ω its angular velocity, then the kinetic energy of rotation of a link is $\frac{1}{2}I\omega^2$. The kinetic energy of the displacement of the center of gravity of the links is contained in $\frac{1}{2}Mv^2$.

Assuming for simplicity an average total thickness s for both flexors and extensors, and considering, as an approximation, each link as an oblong ellipsonid of revolution with semiaxis

$$a = l/2n\,, \quad c = b + s\,, \tag{12}$$

and putting the density ρ equal to one, we have (Appel, 1924)

$$I = \frac{4}{15}\pi a^3 c^2 + ac^4. \tag{13}$$

Hence, from equations (12) and (13),

$$I = \frac{2\pi}{15}\frac{l(b+s)^2}{n}\left[\frac{l^2}{4n^2} + (b+s)^2\right]. \tag{14}$$

Since, practically, $b + s \sim 0{\cdot}2\ l/n$, we may neglect the second term in the bracket and obtain

$$I = \frac{\pi}{30}\frac{l^3(b+s)^2}{n^3}. \tag{15}$$

If we again denote by ϕ the angle made with the vertical by the direction in which the center of gravity of the whole animal is actually propelled by the expansion of the extremities, and if we denote by

$$M_0 = M - 4ls^2 \tag{16}$$

the mass of the animal less the mass of the four extremities, then the work done in lifting the body during the propulsion is equal to

$$W_g = M_0 gl \cos\phi. \tag{17}$$

It may perhaps be argued that since only two extremities out of four are actually involved in the propulsion, we should use, instead of equation (16), the expression $M - 2ls^2$. This, however, is a detail which does not affect the final conclusions, and we shall therefore neglect it here.

Considering the flexor and extensor muscles as approximating plastic, viscous, cylindrical rods of thickness s, and denoting by η the coefficient of viscosity, we have for the viscous force F_v the expression

$$F_v = \frac{3\eta}{L}\frac{dL}{dt}s^2. \tag{18}$$

If v_c is the velocity of contraction of the extensor, then we have approximately

$$\frac{dL}{dt} = v_c. \tag{19}$$

Hence, for each link,

$$F_v = \frac{3\eta s^2}{L}v_c. \tag{20}$$

During an interval of time dt, the displacement of the point of application of F_v is $v_c dt$. Hence the work done during dt is equal to

$$\frac{3\eta s^2 v_c^2}{L}\,dt. \tag{21}$$

The quantity v_c is related to ω, the angular velocity of the link, very roughly by

$$v_c = b\omega\,. \tag{22}$$

If t is the time necessary for a full extension of the extremity, then the average value of ω is

$$\omega = \pi/2t\,. \tag{23}$$

Hence,

$$t = \pi/2\omega\,. \tag{24}$$

From equations (21) and (22) we see that the total viscous work done during the time t in n links is approximately equal to

$$W_v = \frac{3\eta s^2 v_c^2}{L}\,\frac{\pi n}{2\omega} = \frac{3\pi\eta s^2 b^2 \omega n}{2L}. \tag{25}$$

If the extremity unfolds completely during the time t, then the average linear velocity imparted to the body is l/t. During the same interval t each link rotates by an angle π, so that the average angular velocity ω is π/t. Since we are interested here in general functional relations and in orders of magnitude only, we see that v is of the order of magnitude

$$v = l\omega\,. \tag{26}$$

Hence,

$$\omega = v/l\,. \tag{27}$$

The work W, as given by equation (11), must be equal to the sum of $\frac{1}{2}Mv^2$, $4 \times \frac{1}{2}In\omega^2$, the work W_g and W_v. Hence,

$$W = \tfrac{1}{2}Mv^2 + 2In\omega^2 + 4W_v + W_g\,. \tag{28}$$

Introducing equations (11), (8), (15), (27), (17), and (25) into equation (28), we find

$$\begin{aligned} \pi f s_1^2 \varepsilon l = \tfrac{1}{2}Mv^2 &+ \frac{\pi l (b+s)^2}{15n^2}\,v^2 \\ &+ 6\pi s^2 \eta \varepsilon^2 v + M_0 g l \cos\phi\,. \end{aligned} \tag{29}$$

This is a quadratic equation in v.

We shall first investigate the case where the frictional term is so small that it may be neglected. We then have

$$v = \sqrt{\frac{\pi f \varepsilon l s_1^2 - M_0 g l \cos\phi}{\tfrac{1}{2}M + \dfrac{\pi l (b+s)^2}{15n^2}}}. \tag{30}$$

If, as is usually the case (Rashevsky, 1944b), ϕ is large, the cos ϕ term may be neglected. Denoting by M_e the mass of the extremity, remembering that $ls^2 \sim M_e$, and that usually $b << s$, and putting $s_1{}^2/s^2 = \alpha$, we find, from equation (30) using equation (16),

$$v = \sqrt{\frac{\pi f \varepsilon \alpha M_e}{\frac{1}{2} M_0 + [2 + (\pi/15n^2)] M_e}}. \tag{31}$$

For animals which are geometrically similar, $M_e/M =$ const. and $\alpha =$ const. Therefore, for such animals the speed is the same. This is a more general form of a result obtained for a special case by A. V. Hill (1927) (c.f. also Rashevsky, 1944 b). In the absence of geometrical similarity, the speed increases with increasing mass of the extremities, tending to the asymptotic value

$$v_{\max} = \sqrt{1.4 f \alpha \varepsilon}. \tag{32}$$

If, as has been made plausible in a previous paper (Rashevsky, 1944a), we have $s^2 \propto M_0$, and if α is constant, then instead of equation (31) we obtain from equation (30), neglecting the cos ϕ term, and denoting by A and B two constants,

$$v = \sqrt{\frac{Al}{1 + Bl}}. \tag{33}$$

For not too large values of l, we have $v \propto \sqrt{l}$, which, as we have seen (Rashevsky, 1944 b), holds approximately. We find from equation (33)

$$v_{\max} = \sqrt{A/B}. \tag{34}$$

Taking $f \sim 10^7$ dyn cm², $\alpha \sim 1$, and $\varepsilon \sim 0.03$, and assuming $M_e/M_0 \sim 0.03$, as obtained from measurements of pictures of a dog whose speed was determined (Muybridge, 1887), we find from equation (31) $v \sim 2 \times 10^2$ cm sec.$^{-1}$. The actual speed is 12×10^2 cm sec.$^{-1}$. Since the data for f and ε are very uncertain, no better agreement can be expected.

All the above-discussed relations hold, however, only for the initial jump. As has been remarked above, the loss of kinetic energy at the end of each successive jump is not complete, and therefore the theory should be modified for the case of continuous running.

Practically only the vertical component of the velocity v is lost at the end of each jump. Hence in continuous running the extensors of the extremities must provide for each consecutive jump only the amount.

$$\tfrac{1}{2} M v^2 \cos^2 \phi. \tag{35}$$

Expression (35) should be used instead of the first term of the right side of equation (29).

Another thing to be kept in mind is that after each jump the animal does not fold its extremities completely.

Let us make the fairly plausible assumption that at the end of the flight phase the extremity, extended forward, also makes the angle ϕ with the vertical (Figure 1). Since the loss of the vertical component $v\cos\phi$ of the velocity is not instantaneous, the upper part of the extremity will now move not in a horizontal line AA', but will fall somewhat below it (Figure 1). The quantity h in Figure 1b represents the sagging of the center of gravity of the animal during its contact with the ground. It also represents the amount by which the center of gravity must be lifted before each new flight phase, which begins when the extremity is in the position 1c. Defining the angle ψ as in Figure 1b, we see that

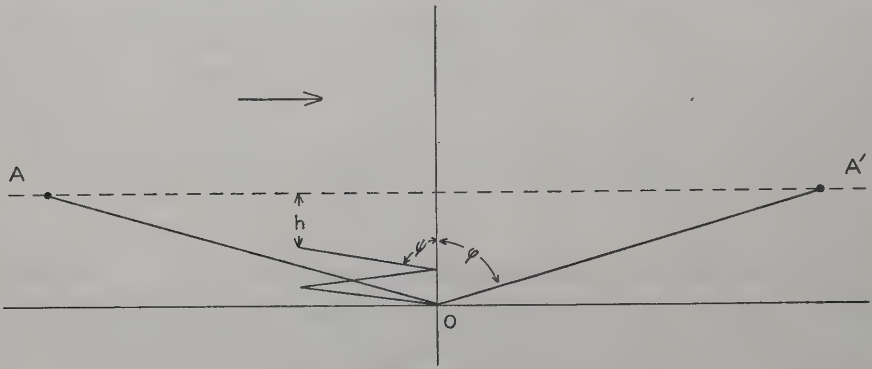

FIGURE 1

$$h = l(\cos\psi - \cos\phi). \tag{36}$$

The circumstance that the extremity is now extended from only a partially flexed position also changes some of the expressions used above. Thus the contraction of each extensor is now not πb, but $[\pi - (\pi - 2\psi)]b = 2\psi b$. Hence, instead of expressions (8) we now have

$$b = \frac{L}{2m\psi} = \varepsilon L; \quad \varepsilon = \frac{1}{2m\psi}. \tag{37}$$

Instead of (11) we have

$$W = 2\psi f s_1^2 \varepsilon l, \tag{38}$$

and instead of (23) and (24) we have, correspondingly,

$$\omega = \frac{\psi}{t}; \quad t = \frac{\psi}{\omega}. \tag{39}$$

Making all those changes we now obtain, instead of equation (29), the following:

$$\begin{aligned} 2\psi f s_1{}^2 \varepsilon l = \tfrac{1}{2} M v^2 \cos^2\phi + \frac{\pi l (b+s)^2}{15 n^2} v^2 \\ + 12 \eta \psi s^2 \varepsilon^2 v + M_0 g l (\cos\phi - \cos\psi). \end{aligned} \tag{40}$$

Equation (40) determines the speed $v_h = v \sin\phi$ of continuous running for prescribed values of ϕ and ψ. What determines those two values? Let us first discuss the factors which determine ϕ.

When the body of the animal, or strictly speaking, its center of gravity, is projected during the flight phase with a velocity v at an angle ϕ with the vertical, the distance which it travels horizontally during the flight phase is given by

$$x = \frac{2v^2}{g} \sin\phi \cos\phi. \tag{41}$$

The time it takes to travel that distance at the speed $v_h = v \sin\phi$ is given by

$$\Delta t = \frac{x}{v_h} = \frac{2v}{g} \cos\phi. \tag{42}$$

The larger the angle ϕ, the greater for a given v is the horizontal velocity v_h. The less also is the work of lifting the body just before the flight phase. Hence it is to the advantage of the animal to make ϕ as large as possible. An upper limit is, however, imposed upon ϕ by the following consideration.

During the interval Δt the extremity must be folded and again extended forward, so as to pass from the position AO in Figure I to the position OA′. If ϕ is too large, then Δt, as seen from equation (42), may become too small to permit this change in the position of the extremity.

The time it takes the extremity to change its position is determined by the force developed by the flexors and extensors and by the inertial and frictional resistances. Let us first consider the inertial resistance.

The work done by the muscular forces in folding the extremity is given by an expression similar to (11) in which, however, we substitute $s_2{}^2$ for $s_1{}^2$, since now the flexors are active. The work of extension is given by equation (11). The total work is given by

$$\pi f \varepsilon l (s_1^2 + s_2^2). \tag{43}$$

The kinetic energy is given by $\frac{1}{2} n I \omega^2$, or, because of (15), by

$$\frac{\pi}{60} \frac{l^3 (b+s)^2}{n^2} \omega^2. \tag{44}$$

The angular velocity is therefore roughly determined by the equation

$$\frac{\pi}{60} \frac{l^3 (b+s)^2}{n^2} \omega^2 = \pi f \varepsilon l (s_1^2 + s_2^2). \tag{45}$$

Since usually $b << s$ and approximately $s^2 = s_1^2 + s_2^2$, we have from (45),

$$\omega^2 = 60 \frac{n^2}{l^2} f \varepsilon. \tag{46}$$

For the time of the complete extension of the extremity we have expression (24). The folding time is of the same order of magnitude. Hence, roughly,

$$\Delta t = \frac{\pi}{\omega}. \tag{47}$$

Introducing (46) into (47), the latter into (42), and solving for $\cos \phi$, we find

$$\cos \phi = \frac{\pi g l}{2 v n \sqrt{60 f \varepsilon}}. \tag{48}$$

Using as plausible values $v = 10^3$ cm sec.$^{-1}$, $f = 10^7$ dyn cm^{-2} (Rashevsky, 1946b.); $\varepsilon = 3 \times 10^{-2}$, $l = 50$ cm, we find $\cos \phi \sim 10^{-2}$, which makes ϕ almost equal to 90°. Actually, ϕ, as observed from some photographs of running animals is about 75°–80°. Hence the inertial forces are not the limiting factor in determining ϕ, and we must conclude, in agreement with A. V. Hill, that the viscous forces are the main source of resistance in continuous running. Let us examine those.

The work of the viscous forces in expanding the extremity is given by expression (25), which, because of (8), may also be written thus:

$$W_v = \frac{3 \pi \eta s^2 \varepsilon^2 L n \omega}{2}. \tag{49}$$

But from (47) we have $\omega = \pi / \Delta t$. Therefore, and because of $Ln = l$, we have

$$W_v = \frac{3\pi^2 \eta s^2 \varepsilon^2 l}{2\Delta t}. \tag{50}$$

Introducing expression (42) into (50) and equating the latter to (43), we find

$$\cos\phi = \frac{3\pi\eta\varepsilon g}{4vf} \tag{51}$$

or

$$\eta = \frac{4vf\cos\phi}{3\pi\varepsilon g}. \tag{52}$$

Now let us consider the factors which determine the angle ψ. If the viscous term in the right side of equation (40) outweighs all others, then ψ cancels out. This would mean that the speed of running is independent of ψ. Actually, although the viscosity term may be much larger than the others, those other terms probably cannot be completely neglected. In that case v is given by the positive root of the quadratic equation (40) and is a function of ψ, and of the other parameters, such as $f, s_1, s, \phi, M, \eta, n, l$, etc. Thus we have

$$v = F(\psi, f, s_1, s, b, \phi, \varepsilon, M, n, \eta, l). \tag{53}$$

We may now ask for the value of ψ which makes v a maximum. This value will be given by the equation

$$\frac{\partial F}{\partial \psi} = 0. \tag{54}$$

If such a maximum exists, then equation (54) determines ψ in terms of the other parameters.

In conclusion let us make a few remarks on what determines the number n of links.

Since ϕ is rather large, the body of the animal is not lifted too much over its normal height above the ground. In moving the extremity forward, it must be at least partially folded and then swung forward. For purely kinematic reasons, the clearance between body and ground must be larger than the length $L = l/n$ of a link. That clearance is approximately of the order of magnitude of $l\cos\phi$. Since, for actually observed values of ϕ (75°–80°), $\cos\phi$ is of the order of 0.25. Hence, approximately, $l/n = 0.25l$, which gives $n = 4$. Actually, due to the parabolic path of the body during the flight phase, the necessary clearance is somewhat larger than $l\cos\phi$, which would reduce to about 3. These considerations throw some light on the fact that the extremities of the rapidly running animals have essentially three links. Animals which, like the elephant or the rhinocerus, are more likely to *walk* fast rather than run, could kinematically afford a smaller number of links. Actually the tarsal part of the extremities in those animals is considerably reduced relative to the femural and tibial parts, which makes the extremity consist of only two major links. For rapid running, however, with a large value of ϕ, less than three links would simply not permit the extremity to move forward during the flight phase.

Another reason for such a structure of the extremity may be the following. If a chain of linked levers is to unfold in such a way that the end A is fixed and the end B follows a prescribed line, then for two links the position of one link prescribes the position of the other. But with three or more links this is not the case. Hence, for a two link extremity, the angular velocities of the two links would have to be exactly coordinated in order to extend the extremity in a given direction. But since, even for independent torques at the joints, the rotations of the links are not independent (Fisher, 1906), such a coordination would be possible, if at all, only for a very special choice of the different constants. In the case of three links this will not be so, as the system as a whole acquires much more flexibility. Little if anything is gained, however, by adding a fourth link.

Another question is why the rear extremities of the animals, which act as the principal "propellers," or rather, "repellers," are shaped as shown in Figure 2a rather than as in Figure 2b. It can readily be seen that in the latter case, at the moment when the extremity separates from the ground, the lower link, rotating counterclockwise, will produce a reaction of the ground in the opposite direction to the direction of the locomotion, thus decreasing the efficiency of the locomotor mechanism (Rashevsky, 1946, pp. 91–92).

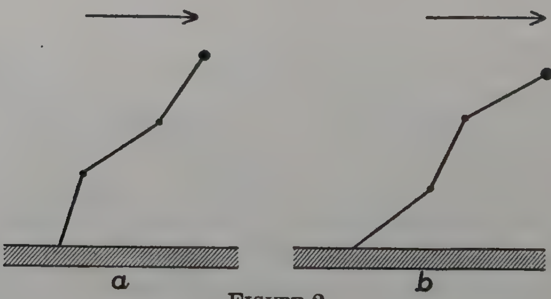

FIGURE 2

All the above, while not constituting a rigorous proof, indicates the plausibility that the shaping of the extremities is determined by requirements of mechanical functions compatible with the simplest structure (Rashevsky, 1943).

If, as A. V. Hill (1927) thinks, and as seems to be borne out by the considerations on page 20 the most important factor in the resistance to locomotion is the muscular viscosity, then we may preserve only the third term in the right side of equation (40) and obtain

$$v = \frac{f s_1^2 l}{6 \eta s^2 \varepsilon}. \tag{55}$$

If enough quantitative data of the desired type were available, we could, by comparison of those data with equations (30), (42), or the general equation which represents the solution of equation (29), draw definite conclusions on the somewhat controversial question of the magnitude of muscular viscosity.

The author is indebted to Dr. H. D. Landahl for a critical discussion of the paper and correction of a few errors.

This work was aided in part by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

LITERATURE

Appell, Paul. 1924. *Traité de Mécanique Rationelle,* Vol. II. Paris: Gauthier-Villars.

Fisher, O. 1906. *Theoretische Grundlagen fur eine Mechanik der Celenden Körper.* Leipzig: Tuebner. C.f. also a series of papers by Browne, W. and O. Fisher, in *Abt. d. Sachs. ger. d. Wis.,* 20, 5–84, 1893; 21, 153–322, 1895; 22, 55–197, 1895; 25, 1–30, 1899; 26, 87–170, 1900; 26, 471–556, 1901; 27, 485–588, 1902; 28, 321–488, 1904; 28, 536–617, 1904.

Hill, A. V. 1927. *Muscular Movement in Man.* New York: McGraw-Hill Book Co.

Muybridge, E. 1887. *Animal Locomotion.* Philadelphia: J. B. Lippincott.

Rashevsky, N. 1943. "Outline of a New Mathematical Approach to General Biology: I." *Bull. Math. Biophysics,* 5, 33–47.

Rashevsky, N. 1944a. "Some General Considerations on the Shape of Quadrupeds." *Bull. Math. Biophysics,* 6, 14–17.

Rashevsky, N. 1944b. "General Theory of Quadruped Locomotion." *Bull. Math. Biophysics,* 6, 17–32.

Rashevsky, N. 1944c. "Suggestions for an Approximate Method for Solving the Equations of Motion of a Chain of Linked Levers." *Bull. Math. Biophysics,* 6, 36–37.

Rashevsky, N. 1946. "Some Considerations on the Structure of Quadruped Extremities." *Bull. Math. Biophysics,* 8, 83–93.

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 10, 1948

SOME MECHANICAL FACTORS IN THE DYNAMICS OF THE THIN-WALLED, SPHERICAL VISCUS*

DANIEL A. BRODY** AND J. P. QUIGLEY
DEPARTMENT OF PHARMACOLOGY, UNIVERSITY OF TENNESSEE, MEMPHIS

Purely mechanical factors involved in the dynamics of the thin-walled, spherical viscus may be elucidated by studying the behavior of an artificial viscus. An equation is developed on theoretical grounds which expresses the pressure-distention characteristics of such a model and apparently corrects the errors contained in similar equations developed by other investigators. A precise definition for wall "tone" is offered. On this basis the mathematics of "tone"-distention relationships have been developed. Experimental investigation of the artificial viscus (spherical rubber balloon) permits the differences in behavior between the ideal and the actual model to be composed, and confirms the validity of our theoretical developments.

Pressures developed within distended hollow viscera reflect not only the effects of well-recognized neuromuscular mechanisms, but also of certain poorly understood factors of a purely physical nature. Experimental investigation and theoretical consideration of artificial hollow viscera have been of some value in separating the solely mechanical factors involved in intralumen pressure production from those related to both the reflex mechanisms and the vital functions of living tissue.

Kelling noted that inflation of a spherical rubber balloon produced a rather rapid rise of pressure to a maximum, followed by a more gradual decline to a prolonged plateau of pressure. Shortly before rupture of the balloon, the pressure dropped precipitously. Osborne, conducting a similar type of investigation, obtained initial results similar to Kelling's. However, if he first "aged" his balloons by subjecting them to repeated inflations, he obtained pressure-distention curves which rose slowly at first and then progressively more

---

* This investigation was financially supported by USPHS grant RG 101.

** The material presented here is part of a thesis for qualification for the degree of M.S. (Pharmacology).

rapidly. A series of inflations of excised dog bladders rendered a similar type of pressure-distention curves. On a purely empiric basis he was able to fit hyperbolae to his curves with moderate success. Sutherland, applying the observations of Henry and of Goy that the strain produced in frog gastrocnemius muscle is a logarithmic function of applied stress, was able to obtain closer fitting curves for Osborne's data. More recently Gianturco showed that the stomachs of intact cats can receive considerable quantities of material without a great rise of intralumen pressure ("receptive relaxation").

On purely theoretical grounds it should be possible to develop an equation which will accurately express the pressures developed within a hollow elastic sphere that obeys Hooke's Law perfectly. Attempts to do so have lead to the following expressions:

$$P=\frac{4Ed_0}{r_0}\frac{r-r_0}{r}; \qquad \text{(Modified from Winton and Bayliss)} \qquad (1)$$

$$P=4Ed_0\frac{r-r_0}{r^2}; \qquad \text{(Brody and Quigley)} \qquad (2)$$

$$P=4Ed_0r_0\frac{r-r_0}{r^3}; \qquad \text{(Frank)} \qquad (3)$$

where P = pressure, E = Young's modulus, d_0 = wall thickness before stretching occurs, r = radius, r_0 = radius at which stretching begins to occur.

Despite the obvious differences in these equations it can be seen that they belong to a family,

$$P=4Ed_0r_0^{n-2}\frac{r-r_0}{r^n}; \qquad (4)$$

n being an integer.

The differences between equations (1), (2), and (3) are illustrated in Figure 1. For small degrees of distention, r is approximately equal to r_0. Therefore, the factor r_0^{n-2}/r^n from equation (4) is essentially independent of n in this range, and the three curves are practically identical. When r is 1% greater than r_0, the P of equation (1) is only 2% greater than the P of equation (3). However, for greater degrees of distention, important differences occur. Taking the maximum value of P in equation (1) to be 100%, the maximum value in (2) will be 25%, and in (3) only 14.8%. Equation (1) attains its maximum at $r = \infty$, (2) at $r = 2r_0$ and (3) at $r = 3/2\ r_0$. Whereas equation (1) approaches its maximum asymptotically, (2)

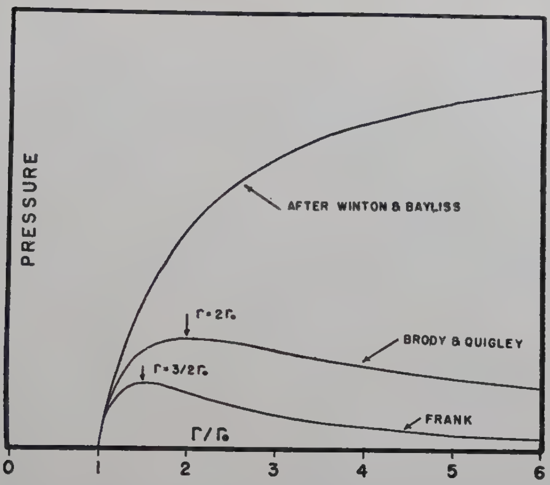

FIGURE 1. Graphic representation of various theoretical pressure-distention relations of the ideal thin-walled elastic sphere. All three curves are drawn to the same scale. The upper curve approaches the top border asymptotically. Other maxima as indicated by vertical arrows.

and (3) attain their maxima at the above finite values of distention following which they approach zero asymptotically.

Reasons for the differences between equations (1), (2), and (3) are evident in their derivations: From the definition of Young's modulus of elasticity E, the reactive tension T, per unit of cross sectional length of an elastic strip which has a thickness d, and has been stretched to a length l, from a resting length l_0, will be

$$T = Ed(l - l_0)/l_0 . \tag{5}$$

Applied to a lune cut from a thin walled elastic sphere, equation (5) becomes

$$T = E_{\text{man}} d(r - r_0)/r_0 . \tag{6}$$

E_{man} is the "manifest" modulus of elasticity for a sheet of material which is stretched equally in all directions. Our theoretical developments show that $E_{\text{man}} = 2E$, a finding which is in agreement with Frank. Thus equation (6) becomes

$$T = 2Ed(r - r_0)/r_0 . \tag{7}$$

Substitution of equation (7) in the well-known formula for pressures developed within a hollow sphere, $P = 2T/r$ (cf. Winton and Bayliss, p. 305), yields

$$P = \frac{4Ed}{r_0}\,\frac{r - r_0}{r}. \qquad (8)$$

Since the wall of an elastic sphere obviously thins on distention, d of equation (7) is a variable. Winton and Bayliss overlook this fact and imply that $d = d_0$, d_0 being the wall thickness before stretching occurs. Frank notes that wall thickness is inversely proportional to the square of the radius and therefore assumes $d = (r_0^2/r^2)\,d_0$. We, on the other hand, emphasize the fact that although true wall thickness varies in the inverse quadratic manner described by Frank, the actual number of elastic fibrils per unit length is inversely proportional to the *first* power of the radius. For this reason we employ the concept of an "effective wall thickness" characterized by $d = (r_0/r)\,d_0$. Substitution of each of these values of d in equation (8) yields equations (1), (2) and (3).

If the radius and intralumen pressure of a thin-walled elastic sphere are known, the wall tension may readily be calculated from $P = 2T/r$. However, it is our opinion that wall tension so calculated is not equivalent to wall "tone" inasmuch as the number of elastic fibrils per unit of length varies with distention.

According to our concept, tone is not the tension exerted by a unit of wall length but rather the tension exerted by a given number of the fibrils which comprise the wall. A convenient number of fibrils to employ as a reference are those contained in one centimeter of unstretched wall (cm_0). Therefore, in the experimental work to be described later in this paper, tone is expressed as gm/cm_0. Such values are determined by multiplying the experimentally determined values of T by the corresponding linear distention factors, r/r_0. Multiplication of equation (7) by the factor r/r_0, and substitution of $d = (r_0/r)\,d_0$ (our concept of "effective wall thickness") yields

$$\text{Tone} = 2Ed_0(r - r_0)/r_0. \qquad (9)$$

Equation (9) is of the same form as equation (7) except that the quantity d_0 enters now instead of d. It should be noted that this is a linear equation, $2Ed_0/r_0$ being the slope and r_0 the r intersect. Similar operations on equation (7), employing $d = d_0$ (implied by Winton and Bayliss) or $d = (r_0^2/r^2)\,d_0$ (Frank) do not lead to linear functions. Since tone represents the pull exerted by a constant number of fibrils, we believe that the linear relation to strain derived by us is correct.

In an effort to test the validity of our equations we conducted a series of balloon inflation experiments in a manner similar to that described by Osborne. Tension was experimentally determined by substituting measured values of pressure and radius in the equation $P = 2T/r$. "Tone" was then calculated by multiplying each value of tension by a corresponding linear distention factor, r/r_0.

Figure 2 represents the results of a typical experiment. Although the "tone" curve is not a straight line because rubber is not a perfectly elastic material, as a rough approximation we may represent each of the first two portions of that curve by a segment of straight line. Straight lines were graphically fitted to these portions and extended until they intersected the abscissa. The two points of intersection constitute respectively r_0 and r_0'. The slopes are equivalent respectively to $2Ed_0/r_0$ and $2E'd_0'/r_0'$ (Cf. equation 9). Wall thickness before stretching, d_0, being known, values of Young's modulus (E and E') may be calculated from the slopes of the two portions under consideration. However in the case of the second portion of linearity the correction, $d_0' = (r_0/r_0')d_0$, must be made. The next step in curve fitting involves calculation of $4Ed_0$ and $4E'd_0'$ from the two slopes and r_0 and r_0' respectively. Substitution of these various factors in equation (2) gives two equations which agree fairly well with the observed pressures in the regions where they are applied.

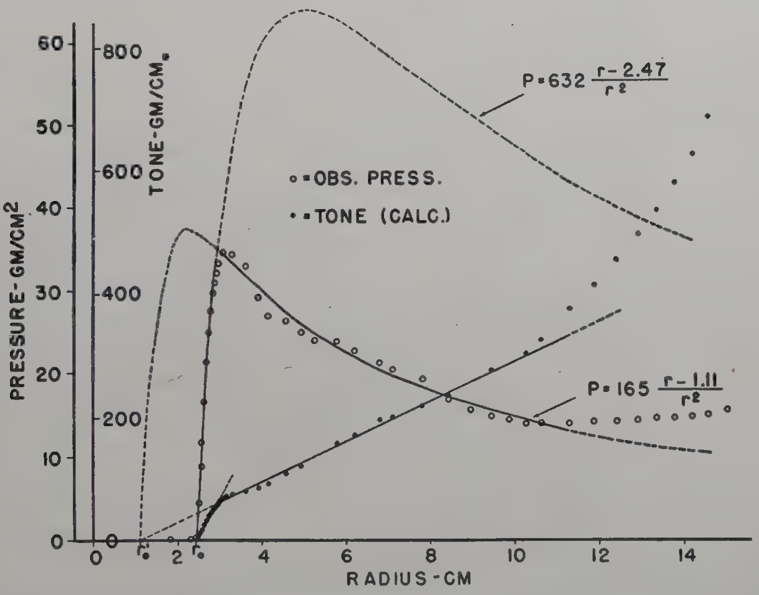

FIGURE 2. Correlation between theoretical and actual pressures produced by distention of an artificial thin-walled, spherical viscus (rubber balloon). Solid portions of the straight lines and pressure curves indicate the regions where our equations (2) and (9) in the text may be applied to the experimental data.

This method of reducing data also permits calculation of Young's modulus in regions where it is variable (d Tone$/dr \neq$ constant) by graphically fitting tangents to the "tone" curve at various points under consideration and treating them in the manner outlined in the preceding paragraph. It is probable that the increasing slope of the "tone" curve beyond the second linear portion is due in part to reorientation of elastic fibrils in the directions of stress. However, since the stress is uniform in all directions of the surface of the balloon, the errors arising from this source in our experiments must be considerably less than those which would result from the application of one dimensional stress ordinarily employed in investigating elastic properties.

Hollow viscera are neither spherical nor perfectly homogenous, and in their *in vivo* situation factors other than contraction of their wall musculature contribute to intralumen pressure production. However such organs as heart, stomach, and bladder, particularly when distended, approximate the spherical contour sufficiently to warrant some application of the foregoing mathematical developments to their mechanics. In our hands, interpretation of gastric pressure-filling curves in the light of equation (2) has proved valuable, and we have been able to demonstrate important physical factors in the phenomenon of "receptive relaxation" (Brody and Quigley).

LITERATURE

Brody, D. A. and J. P. Quigley. 1947. "Some Physical Factors in Receptive Relaxation." *Fed. Proc.* 6 No. 1, 82–83.

Frank, O. 1910. "Dehnung einer Kugelformigen Blase." *Ztschr. f. Biol.*, 54, 531–532.

Gianturco, C. 1934. "Some Mechanical Factors of Gastric Physiology." *Am. J. Roentegenol. and Radium Therapy*, 31, 735–744.

Kelling, G. 1903. "Untersuchen über die Spannungzustände der Bauchwand, der Magen – und Darmward." *Ztschr. f. Biol.*, 44, 161-258.

Osborne, W. A. 1909. "The Elasticity of Rubber Balloons and Hollow Viscera." *Proc. Royal Soc. of London* (B), 81, 485-497.

Sutherland, W. 1909. "Note on Foregoing Paper by W. Osborne." *Ibid.*, 497–499.

Winton, F. R. and L. E. Bayliss. 1935. *Human Physiology*. Philadelphia: P. Blakiston's Son and Co.

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 10, 1948

A MECHANISM FOR OPTIC NERVE CONDUCTION AND FORM PERCEPTION: I

JAMES T. CULBERTSON
THE UNIVERSITY OF CHICAGO

This paper describes a mechanism for (1) bottle-neck optic nerve conduction and (2) the recognition of visual spatial forms. (1) In this mechanism the w retinal receptor neurons are in one-one causal relation to a set D of w central neurons, the connecting optic nerve containing less than w fibers. (2) Also a set ϕ of μ spatial forms (herein defined) is in the one-one causal relation to a set F of μ central neurons so that if f_ι (any given number of F) fires, then the corresponding ϕ_ι has occurred in the retinal image. Only ϕ_ι can fire f_ι, but f_ι may fire for any position, size or orientation of ϕ_ι on the retina, with the restriction that ϕ_ι not be smaller than a minimum size which is a function of retinal position. Neuron economy is considered throughout.

I. Hypothetical Retina, Optic Nerve and Central Retina

For convenience we will arbitrarily assume that for some choice of the time $t = 0$, no neuron fires at non-integral values of t in the nerve net discussed. The interval from the start of a "time of action" in any neuron to the end of the succeeding synaptic delay at any axon synapse of that neuron is assumed constant and equal to .0005 sec., and this interval δ is taken as the unit of time. (McCulloch & Pitts, 1943, Rashevsky, 1946; p. 30). We shall also follow the notations of those papers. The $\sum$ and π refer to the *logical* sum and product except where the context indicates otherwise.

There are about 137 million receptors in one retina but fewer receptor neurons, as most of the latter extend to a plurality of receptors. In the hypothetical monocular network described below we will take the number w of retinal receptor neurons as 25 million and assume that each has just one receptor. We describe first the neural connections whereby these w photoreceptors, illustrated by set A in Figure 1, are in one-one causal relation to the similarly illustrated central set C of w neurons. (See also H. D. Landahl, 1939).

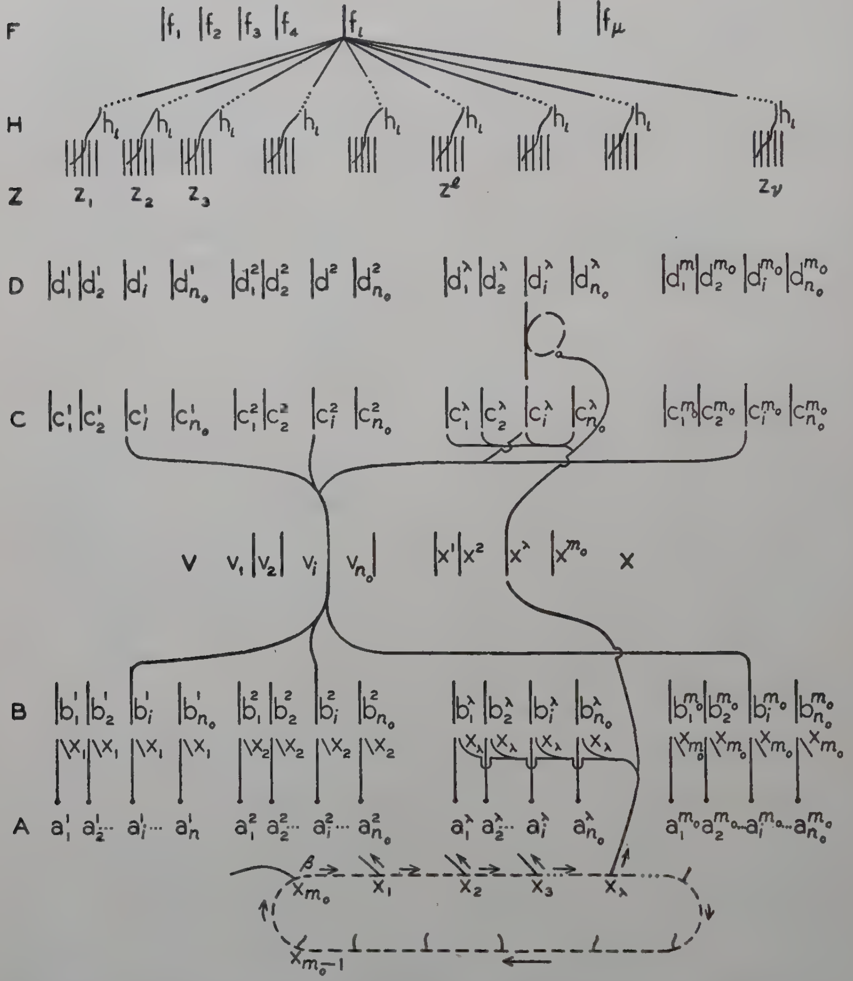
F
f₁ f₂ f₃ f₄ f_l f_μ
H
h_l
Z
z₁ z₂ z₃ z^l z_ν
D
d¹₁ d¹₂ d¹ᵢ d¹ₙ₀ d²₁ d²₂ d²ᵢ d²ₙ₀ d^λ₁ d^λ₂ d^λᵢ d^λₙ₀ d^m₀₁ d^m₀₂ d^m₀ᵢ d^m₀ₙ₀
C
c¹₁ c¹₂ c¹ᵢ c¹ₙ₀ c²₁ c²₂ c²ᵢ c²ₙ₀ c^λ₁ c^λ₂ c^λᵢ c^λₙ₀ c^m₀₁ c^m₀₂ c^m₀ᵢ c^m₀ₙ₀
V
v₁ v₂ vᵢ vₙ₀
x¹ x² x^λ x^m₀
X
B
b¹₁ b¹₂ b¹ᵢ b¹ₙ₀ b²₁ b²₂ b²ᵢ b²ₙ₀ b^λ₁ b^λ₂ b^λᵢ b^λₙ₀ b^m₀₁ b^m₀₂ b^m₀ᵢ b^m₀ₙ₀
x₁ x₂ x_λ x_m₀
A
a¹₁ a¹₂ a¹ᵢ a¹ₙ a²₁ a²₂ a²ᵢ a²ₙ₀ a^λ₁ a^λ₂ a^λᵢ a^λₙ₀ a^m₀₁ a^m₀₂ a^m₀ᵢ a^m₀ₙ₀
β
x_m₀ x₁ x₂ x₃ x_λ
x_m₀−1

FIGURE 1. For correspondence with the text the following changes should be made in this figure. Neuron sets labeled $z_1, z_2, z_3, \cdots z_l \cdots z_\nu$ should be labeled $z^1, z^2, z^3, \cdots z^l \cdots z^\nu$. In the large cycle there should be *three* internuncials between x_1 and x_2, between x_2 and x_3, between x_3 and x_4, etc., and finally between x_{m_0-1} and x_{m_0}, and between x_{m_0} and x_1. There should be *two* internuncials between β and x_1.

In the cycle between levels C and D the impulses run clockwise. Although the connecting line is omitted, dendrite b_i^λ is part of the neuron v_i.

Set A is divided into m_0 equal subsets

$$\begin{array}{l} A^1(a_1^1, a_2^1 \cdots a_i^1 \cdots a_{n_0}^1) \\ A^2(a_1^2; a_2^2 \cdots a_i^2 \cdots a_{n_0}^2) \\ \cdot \\ \cdot \\ \cdot \\ A^\lambda(a_1^\lambda, a_2^\lambda \cdots a_i^\lambda \cdots a_{n_0}^\lambda) \\ \cdot \\ \cdot \\ \cdot \\ A^{m_0}(a_1^{m_0}, a_2^{m_0} \cdots a_i^{m_0} \cdots a_{n_0}^{m_0}) \end{array}$$

of n_0 neurons each, so that a_i^λ denotes the ith member of the λth subset A^λ. Thus $m_0 n_0 = w$, and as a particular case we will take $n_0 = 10^6$ and $m_0 = 25$. Neuron set A is in one-one relation to a similarly subdivided set B of w dendrites so that a_i^λ has one end bulb on b_i^λ whose threshold is 2. The retina contains also a cycle of km_0 neurons where $k = 4$ is the refractory period for neurons in the net. (Since $k = 4$ the maximum possible discharge frequency is 500/sec.). The first neuron in the cycle is designated by β and the $(k\lambda)$th neuron by x_λ. Neuron x_λ has one end bulb on b_i^λ so that $a_i^\lambda(t-1) \cdot x_\lambda(t-1) \cdot \rightarrow \cdot b_i^\lambda(t)$ which is read, "If a_i^λ fires at $t-1$ and x_λ fires at $t-1$ then b_i^λ fires at t." The arrow (→) is used as the implication symbol instead of the horseshoe.

In the inactive cycle let just β fire for any reason at some time (so as to start the cycle) and thereafter let $q(t) \cdot \equiv \cdot p(t-1)$ where p and q are consecutive cycle neurons and p precedes q. Thus only one impulse is passing through the cycle. Choosing any time at which β fires as $t = 0$ we have

$$\beta(0), \tag{1}$$

$$\beta(lkm_0); \quad l = 0, 1, 2, \cdots [k = 4, m_0 = 25], \tag{2}$$

$$x_1(k-1), \tag{3}$$

$$x_\lambda(t) \cdot \equiv \cdot t = k(\lambda + lm_0) - 1. \tag{4}$$

The period of the cyclical impulse is $km_0\delta$. Receptor neuron a_i^λ is associated with $K-1$ neurons as shown in Figure 2, giving

$$b_i^\lambda(t) \cdot \equiv \cdot x_\lambda(t-1) \cdot \sum_{j=1}^{K} a_i^\lambda(t-j), \tag{5}$$

where $\sum$ indicates the logical sum of the K propositions. We will take $K = 4$.

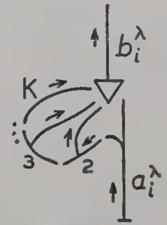

FIGURE 2

The optic nerve contains $n_0 + m_0$ neurons. There are $n_0 = 10^6$ neurons each designated $v_i \, (i = 1, 2, 3, \cdots n_0)$. Neuron v_i has the m_0 dendrites $b_i^1, b_i^2, \cdots b_i^\lambda \cdots b_i^{m_0}$. There are m_0 neurons each designated $x^\lambda \, (\lambda = 1, 2, 3, \cdots m_0)$. Cycle neuron x_λ has an end bulb on x^λ. Thus

$$v_i(t) \cdot\equiv\cdot \sum_{\lambda=1}^{m_0} b_i^\lambda(t), \tag{6}$$

$$x^\lambda(t) \cdot\equiv\cdot x_\lambda(t-1). \tag{7}$$

Proposition (6) merely states that v_i fires whenever any one of its m_0 dendrites fires.

Let C be a set of w central neurons (a "central retina") in one-one relation to A and likewise divided into its corresponding m_0 subsets of n_0 neurons each. Neurons v_i and x^λ each have one end bulb on c_i^λ and the threshold of c_i^λ is 2; therefore

$$c_i^\lambda(t) \cdot\equiv\cdot v_i(t-1) \cdot x^\lambda(t-1). \tag{8}$$

Thus if c_i^λ fires at t then a_i^λ fired at either $t-2$, $t-3$, $t-4$, or $t-5$, which may be written

$$c_i^\lambda(t) \rightarrow \sum_{j=2}^{K+1} a_i^\lambda(t-j). \tag{9}$$

This gives complete specificity (spatially) for the central discharges, no member of the central retina firing unless the corresponding member of the retina fires.

We see that a_i^λ may fire and not cause c_i^λ to fire since at $t = k$ only members of B^1 may fire, at $t = 2k$ only members of B^2 may fire, etc., so that members of B^λ may fire only once every $km_0\delta$. If a_i^λ fires once the probability p that this will cause c_i^λ to fire is K/km_0. Normally, however, any effective stimulus gives rise to a volley of impulses from each receptor affected. If a_i^λ fires a volley of impulses the probability P that this volley will cause c_i^λ to fire is, of course, greater than

p. Let f_1 be the average discharge frequency of a_i^λ during the first $km_0\delta$ after the volley starts, that is, the number of firings during the first $km_0\delta$ divided by km_0. Also let f_2 be the average frequency during the second $km_0\delta$, etc., and finally let f_M be the average frequency during the last $km_0\delta$ after the volley starts and in which there is some member of the volley. Then $P = 1 - \prod_{i=1}^{M} (1 - Kf_i)$, if we assume that Kf_i is the probability that some member of the volley during the ith $km_0\delta$ causes c_i^λ to fire.

Since the subsets of A send impulses through the optic nerve successively the latter contains $n_0 + m_0 = 1{,}000{,}025$ fibers, but if the subsets sent their impulses through simultaneously the nerve would contain $n_0 m_0 = 25{,}000{,}000$ fibers. S. L. Polyak (1941, p. 447) estimates about 10^6 fibers in the optic nerve.

Using the above mechanism with $w = 2.5 \times 10^7$ we see that the number N of optic nerve fibers has the minimum value of 10^4, since minimizing $N = m_0 + w m_0^{-1}$ we get $dN/dm_0 = 1 - w m_0^{-2} = 0$ so that $m_0 = n_0 = \sqrt{w}$ and $N_{\min} = 2\sqrt{w} = 10{,}000$. As N decreases, however, (from $m_0 = 1$) the time $\mathcal{T} = km_0\delta$ for the passage of impulses from all the subsets increases. In the net described $\mathcal{T} = .05$ sec, and if N was a minimum we would have $\mathcal{T} = 10$ sec.

In C the m_0 subsets fire in succession, each firing once every $km_0\delta$, and no two firing at the same time. To get the neuron set D in which all m_0 subsets fire simultaneously let D, the "synchronized retina", consist of w neurons in one-one causal relation to C so that c_i^λ is connected to d_i^λ by a cycle of k neurons with an inhibitory bulb from x^λ as shown in Figure 1. Thus in D all m_0 subsets fire simultaneously every $k\delta$, and if c_i^λ fires at t then d_i^λ fires at the m_0 times $t + 2, t + 6, t + 10, \cdots t + (m_0 - 1)k + 2$ and conversely. This may be expressed by

$$c_i^\lambda(t) \cdot\equiv\cdot \prod_{j=0}^{m_0-1} d_i^\lambda(t + j + 2)\,. \tag{10}$$

The firings in D are in one-one causal relation to the firings in A so that there is complete specificity (spatially) for these central discharges, no member of D firing unless the corresponding member of the retina fires. Thus we have

$$d_i^\lambda(t) \cdot\rightarrow\cdot \sum_{j=0}^{m_0 k} a_i^\lambda(t - j - 4)\,. \tag{11}$$

The above mechanism for optic nerve conduction and central representation leads directly to the mechanism for form recognition described below. The retinal impulses are "funneled" successively through the one set v in the optic nerve. Now in somewhat the same way impulses in D "funnel" successively through a set z of central neurons. In this second mechanism, however, there is not just the one set z, but many such sets $z^1, z^2, \cdots z^l, \cdots z^\nu$, (Figure 1) so that many such funneling processes are occurring at the same time. When impulses "funnel" successively the same term will be used for the pathways over which they funnel; so we will say, for instance, that the m_0 subsets of A "funnel" successively through the set v, and we will use this term whenever sets of neurons are related in this way. It is understood that if m sets funnel through one set, there is an associated cycle with firing intervals as described above.

II. Hypothetical Mechanism for the Reproduction of Forms

Henceforth for simplicity let the w $(= 2.5 \times 10^7)$ receptors be equally spaced in a square array of rows and columns. Leaving the mechanism described in section I unaltered let the "synchronized retina" D be geometrically similar to the retina, the cell body of d_i^λ being in the same relative position as the receptor of a_i^λ. *This is for simplicity of explanation only* since the cells of D may have any relative positions whatever.

To illustrate first reproduction involving translation only, choose any m square areas within D (the sides of each square being parallel and perpendicular to the sides of D) containing $n = 225$ neurons and let the m sets $s^1, s^2, \cdots s^\kappa \cdots s^m$ inclosed by these squares funnel successively through a similar square set z of n cells after D. Denote by s_{ij} the member of the ith row and jth column in each of these m sets, use a similar notation for z, and let $s_{ij}{}^\kappa$ have one end bulb on z_{ij} so that

$$z_{ij}(t) \cdot\equiv\cdot \sum_{k=1}^{m} s_{ij}{}^\kappa(t-1) \cdot x^\kappa(t-1), \tag{12}$$

where x^κ is the cycle neuron corresponding to s^κ. Here $\mathcal{T} = mk$. Superimpose any solid figure, say a T on z and let the ω cells inside it each have an excitatory bulb on some neuron h whose threshold is ω and each cell outside have an absolute inhibitory bulb on h. (Less strict conditions for the firing of h are given below.) Neuron h fires at $t + 1$ for only this one firing pattern (call it P_{T}) in z at t. Define the activity matrix $P(z, t)$ as follows. Pattern $P(z, t)$ is a square matrix of $n = 15^2$ elements a_{ij} in which $[a_{ij}] = 1$ if $z_{ij}(t)$ is true and $a_{ij} = 0$ if $z_{ij}(t)$ is false. (Landahl and Runge, 1936; Landahl, 1947.). The neuron h fires at $t + 1$ if and only if $P(z, t) = P_{\mathrm{T}}$.

Because of the above funneling it follows that any given value of t, $P(z, t) = P(s^{\kappa}, t-1)$ for some value of κ. If h fires at $t + 1$ then at $t-1$ some one of m different patterns in D were identical to $P_{\mathbf{T}}$. Thus there are m different positions on the retina in which an image of **T** (of proper size and orientation) may be projected so as to cause h to fire.

Let the square area on D inclosing s^{κ} be divided into n equal small squares and let there be one member of s^{κ} in each small square. This large square area divided into smaller squares will be called a *mapping*. In general a mapping is any square area on D divided into $n = 225$ equal small squares such that at least one member of D is in each small square. In Figure 3 one mapping is illustrated and n is taken as 25 in order to make a simpler diagram. To illustrate the general reproduction of forms, replace the m special mappings of the preceding paragraph by any m mappings $M^1, M^2 \cdots M^{\kappa} \cdots M^m$ differing generally in size, position and orientation, and let the m sets $s^1, s^2, \cdots s^{\kappa} \cdots s^m$ each consist of all neurons within one mapping, i.e., s^{κ} consists of all neurons within M^{κ}. As mappings may overlap, some neurons in D may be in more than one of these m sets. Designating arbitrarily one edge of each mapping as the top and then numbering rows and columns in the conventional way (mirrored mappings are excluded), any small square in M^{κ} is in a numbered row and numbered column. In M^{κ} *each neuron* in the square in the ith row and jth column is designated s_{ij}^{κ}. Each of these neurons i.e., each s_{ij}^{κ} has one end bulb at a synapse on z_{ij}. At that synapse there is one end bulb from each s_{ij}^{κ} and no other end bulbs, and the threshold equals 1/2 the number of these end bulbs. Hence this synapse fires at t if and only if at least half of the s_{ij}^{κ}'s fire at $t-1$. There are, of course, m

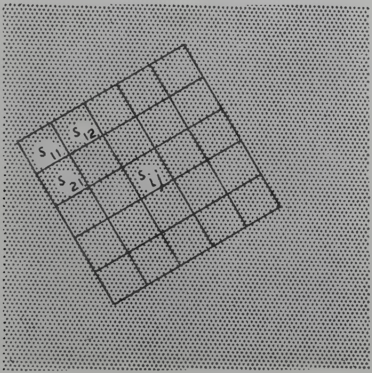

FIGURE 3

such synapses (functionally separate collections of end bulbs) on z_{ij}, say on m different dendrites of z_{ij}. Then $P(s^\kappa, t)$ i.e., the pattern or activity matrix of s^κ at t is defined as a square matrix of $n = 15^2$ elements in which $a_{ij} = 1$ if at least half of the s_{ij}^κ's fire at t and $a_{ij} = 0$ if less than half fire at t. For any value of t, just as before, $P(z, t) = P(s^\kappa, t{-}1)$ for some value of κ.

Thus there are m different variations of position, size, rotation on the retina in which an image of a **T** may be projected so as to cause h to fire.

In the hypothetical mechanism described below there is not just one funnel through one set z but $\nu = 100$ funnels through the ν sets $z^1, z^2, \cdots z^l \cdots z^\nu$ (see Figure 1). We have $m \cong 640,000$ and this is the same for all the ν funnels, so that $\mathcal{T} \cong 1280$ sec. for all funnels. The value of $\mathcal{T}$ will seem absurdly large especially in regard to the short reaction times in form recognition, until it is shown later how the entire cycle need not be run through, but instead the impulse may pass through part of the cycle and then jump to another part of the cycle in such a way as to give short reaction times. The accessory "attention" mechanism to omit parts of the cycle is described later. Also, the large value of m makes the number of synapses on z_{ij} too large for the anatomical evidence, but this is easily corrected later after the main outline of the mechanism has been given.

For simplicity all the ν sets at level Z (see Figure 1) are identical in structure, and the ν sets at level H are identical in structure and also in the contacts they make with the Z level. Only one neuron in each set at level H is shown.

The total number $\mathcal{N}$ of mappings which give the sets s in the mechanism is $\mathcal{N} = \nu m = 6.4 \times 10^7$. Suppose at the H level some neuron u has contacts so as to fire at $t + 1$ if and only if $P(z^l, t) = P_{\mathbf{T}}$. Then there would be a set X of $\nu = 100$ similar neurons, one above each z^l, such that there are 6.4×10^7 different variations of position, size, orientation on the retina in which an image of a **T** may be projected so as to cause some member of X to fire. *No member of* X *fires for any* P(z, t) *which does not equal* $\mathrm{P}_{\mathbf{T}}$. Level F is an optional addition to the mechanism such that some *one* f fires if and only if any member of X fires. If we include level F in the nerve net, then there are $\mathcal{N}$ variations in which the image **T** may be projected upon the retina so that the one neuron f fires. No other image can cause f to fire, and no other neuron at level F fires for that image.

The sets at level Z are identical and the sets at level H are identical but each set, s, from any mapping passes through just one of the ν funnels. If we include level F in the nerve net, then there are

$\mathcal{N}$ variations in which the image **T** may be projected upon the retina so that the one neuron f fires. No other image can cause f to fire, and no other neuron at level F fires for that image.

The sets at level Z are identical and the sets at level H are identical, but each set s from any mapping passes through just one of the ν funnels.

The particular value of $\mathcal{N}$ given above depends upon a systematic way in which the mappings are applied to D. All numerical values stated are arbitrary but illustrate the requirements that every part of D be covered by at least one mapping, that the area of the smallest mapping covering any point in D is greater for points near the periphery than for points near the center, and that the whole range of variations in area, position, orientation be filled in as uniformly as possible.

That edge of D which is causally related to the upper edge of the visual field will be called the *top* of D. Consider a mapping whose top is parallel to the top of D. Furthermore, the top of that mapping is nearer to the top of D than the bottom of that mapping. Such a mapping we shall call *upright*. There are $m = \mathcal{N}/\nu$ of these as follows.

The smallest upright mappings each have an area of 225, taking the distance between two consecutive neurons in a row or column of D as the unit of distance. Multiplying by 1.1 we get the area of the next largest mappings, and multiplying this again by 1.1 we get the area of the next largest, etc. In this way the area of any upright mapping is $225\ (1.1)^{\gamma}$ where $\gamma = 0, 1, 2, \cdots 121, 122$ as $\gamma = 122$ gives the largest possible upright mapping, so we have upright mappings of 123 different sizes. The center squares of upright mappings having the same area do not overlap but fill a square area and the center of this square area is the center of D.

Let $\mathcal{N}_{\gamma}$ be the number of upright mappings of area $225\ (1.1)^{\gamma}$ and let $\mathcal{N}_{\gamma}$ be a maximum such that

$$R \geqq \mathcal{N}_{\gamma} \leqq (10 + \gamma)^2$$

where R is the greatest number of upright mappings of area $225\ (1.1)^{\gamma}$ that can be mapped on D so that their center squares do not overlap. Then for each value of $\gamma \leqslant 81$ there are $(10 + \gamma)^2$ mappings whose area is $225\ (1.1)^{\gamma}$ so that $\sum_{\gamma=0}^{81} \mathcal{N}_{\gamma} = 10^2 + 11^2 + 12^2 + \cdots + 91^2 = (91 \cdot 92 \cdot 183 - 10 \cdot 11 \cdot 21)/6 = 255{,}001$ mappings. For $\gamma > 81$ the values of $\mathcal{N}_{\gamma}$ decrease somewhat irregularly and we have $\sum_{\gamma=82}^{122} \mathcal{N}_{\gamma} = 87^2 + 82^2 + 78^2 + 74^2 + 69^2 + 67^2 + 62^2 + 59^2 + 55^2 + 52^2 + 49^2 + 46^2 + 43^2 + 40^2 + 38^2 + 35^2 + 33^2 + 31^2 + 29^2 + 27^2 + 25^2 + 22^2 +$

$21^2 + 20^2 + 19^2 + 17^2 + 16^2 + 14^2 + 13^2 + 12^2 + 11^2 + 9^2 + 8^2 + 7^2 + 6^2 + 5^2 + 5^2 + 4^2 + 3^2 + 2^2 + 1 = 66{,}207$. For the total of all upright mappings we then have $\sum \mathcal{N}_\gamma = 321208 \cong 3.2 \times 10^5$. We get all the mappings, upright and non-upright, by rotating each upright mapping through the $\nu = 100$ angles $2l\pi/\nu$ $(l = 1, 2, \cdots \nu)$ so that the total number of these mappings is 3.2×10^7 Any such orientation of an upright mapping is defined as giving a mapping even though some small squares of the rotated area may fall entirely outside D. Mappings at an angle $.02l\pi$ give the sets which funnel through z^l. Thus the sets of all mappings at 3.6° funnel through z^l, the sets of all mappings at 7.2° funnel through z^2, etc., and finally the sets of all upright mappings funnel through $z^{\nu=100}$.

The above mappings are *half* the total number $\mathcal{N}$. The other mappings are made on D', a manifold exactly similar to D. We add w neurons at the same level as D to form D'. Each neuron having x end feet on any neuron in D has x end feet on the corresponding neuron in D' so that $P(D, t) = P(D', t)$. For each mapping M on D we derive the mapping M' on D' by translating M so that its center point is moved $\sqrt{2}/2(1.1)^\gamma$ units to the top right corner of its center square $s_{8,8}$. Remove this mapping from D to the same position on D' to give the mapping M'. Thus $\mathcal{N} = 2 \sum \mathcal{N}_\gamma$.

We will suppose conditions arranged so that only **T** shaped images are projected on the retina one at a time, and that each is projected for the time interval $\mathcal{T} = mk$. Ignoring end organ adaptation we will suppose that maximum discharge frequencies always occur and continue throughout the time of stimulation. We wish to show that (1) certain small variations of any **T** image which causes neuron f to fire will also cause f to fire; then more generally that (2) continuous variations of the image will cause f to fire. This description of the mechanism will be continued in a subsequent paper.

This work was aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

LITERATURE

Landahl, H. D. 1939. "Contributions to the Mathematical Biophysics of the Central Nervous System." *Bull. Math. Biophysics*, 1, 95–118.

Landahl, H. D. and Runge, Richard. 1946. "Outline of a Matrix Algebra for Neural Nets." *Bull. Math. Biophysics*, 8, 75–81.

Landahl, H. D. 1947. "A Matrix Calculus for Neural Nets: II." *Bull. Math Biophysics*, 9, 99–108.

McCulloch, Warren S. and Walter Pitts. 1943. "A Logical Calculus of Ideas Immanent in Nervous Activity." *Bull. Math. Biophysics*, 5, 115–133.

Polyak, S. L. 1941. *The Retina.* Chicago: The University of Chicago Press.

Rashevsky, N. 1946. "The Neural Mechanism of Logical Thinking." *Bull. Math. Biophysics*, 8, 29–40.

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 10, 1948

A STATISTICAL APPROACH TO THE THEORY OF THE CENTRAL NERVOUS SYSTEM

ALFONSO SHIMBEL AND ANATOL RAPOPORT
THE UNIVERSITY OF CHICAGO

A "probabilistic" rather than a "deterministic" approach to the theory of neural nets is developed. Neural nets are characterized by certain parameters which give the probability distributions of different kinds of synaptic connections throughout the net. Given a "state" of the net (i.e., the distribution of firing neurons) at a given moment, an equation for the state at the next moment of quantized time is deduced. Certain very special cases involving constant distributions are solved. A necessary condition for a steady state is deduced in terms of an integral equation, in general non-linear.

I.

It is becoming increasingly evident to those engaged in developing the "neural net" approach to psychology that the methods used in the early phases of development of the theory will need to be supplemented in future work by a theory taking greater cognizance of the anatomy of organisms.

This need arises largely from the following shortcomings of specifically constructed neural nets:

1. It can be shown that for any postulated neural net, whose "firing pattern" is isomorphic to the invariant aspects of a given psychological phenomenon, there can be constructed an infinity of alternative neural nets isomorphic to the same phenomenon.
2. Some of the neural nets require a greater number of neurons in their structure than is contained in the entire nervous system.
3. Most of the neural nets thus far considered are so highly specific in their structure that the failure of even one neuron to function renders the entire mechanism useless.

The first of the above considerations raises the problem of determining which neural nets (of an infinity of alternatives) are indeed present and functional in the nervous system of the organism. The answer to this problem probably rests upon the invention of new laboratory techniques which will give a practicable procedure of tracing directly the neural circuits. Such techniques, however, will probably be aided largely by less direct inferential methods such as those, for example, which are currently employed by the physiological psychologists.

The second and third considerations are more serious weaknesses in the specific net work theory. The second clearly rules out some of the postulated neural nets, while the third raises an uneasy question, namely, can we expect that the genetic constitution of a zygote carries a sufficient amount of "information" to predetermine the growth of a highly complex nervous system consisting of a tremendous number of minutely specific neural structures?

It would be meaningless to say that this is either probable or improbable since any statement about the probability of an event requires a knowledge not only of the event itself but of all its alternatives. Since such knowledge is lacking, the authors will be content to express a mere suspicion of its improbability. The suspicion is founded on the following evidence:

1. Lasheley's experiments on rats (Lasheley, 1926) demonstrated that the maze learning ability does not depend upon any specific region of the cortex but is roughly proportional to the *amount* of cortical tissue possessed by the animal. These experiments tend to refute the "specific connection" hypothesis at least in those animals.
2. Identical twins of the same genetic constitution and remarkably similar macroscopically differ on the microscopic or the near microscopic level, for example, in their fingerprints (Newman, 1940). This evidence suggests that the genes may not predetermine the details of microscopic structure but may exercise only a "statistical influence", (McCulloch & Pitts, 1947) a "bias" on the growth of tissue.
3. From the point of view of the "specific connection" hypothesis, bearing in mind the mechanisms of inheritance, one would expect that a great many psychological traits would either be present in an organism or entirely lacking. In reality organisms are found to possess traits in almost any degree of "intensity" or "facility".

A statistical approach to the structure of the nervous system may be able to cope with these difficulties. Two distinct avenues of development are suggested: (1) a statistical description of the evolution of the nervous system and, (2) a statistical description of the functioning of a neural net. The authors, after considering some questions arising in both types of approach, have decided to start with the latter. Starting with "completely random" structures with only the crudest properties of neural nets, it is the intention of the authors to obtain "order out of chaos" (as N. Wiener once said it). If we are fortunate to be able to describe some overall properties of nets which lead to a type of functioning resembling actual nervous systems, we shall then attempt to formulate the growth biases which lead to the formation of such nets. In this way it is hoped that the two approaches may become unified.

We are thus led to study nets which exhibit certain properties by virtue of "tendencies" and "biases" in their connections and structure. In classical physics an analogous task was undertaken in the study of the behavior of gases. The kinetic theory has greatly elucidated the problem by its use of "parameters" such as density, velocity distribution, etc., which obviate the need of taking into account the disposition of each molecule of the gas. In a similar way we propose to use parameters which will describe only "gross" properties of a neural net.

II.

In order to facilitate the mathematical symbolization of the problem and to illustrate the approach with a specific formulation, it will be necessary for us to define some components of nervous tissue in a highly schematized way, taking into account only those aspects of the components which are pertinent to our formulation. Thus, although dignified by a biological nomenclature, our components will be frankly mathematical constructs stripped of all properties except those specified in the following definitions.

Neuron: A point in space characterized by one of two alternative states, namely, *firing* or *not firing*, and by an integer called the *threshold*.

Bulb: A point in a region immediately adjacent to a neuron, characterized by one of two alternative states, namely, *active* or *not active*.

Axone: A relation between a neuron and a set of bulbs, such that if the neuron is firing, all of the bulbs of the set are active *at the same time*. The bulbs associated with a neuron in this way will be said to originate at that neuron. They will also be called the terminal bulbs of the axone.

Synapse: The region immediately adjacent to a neuron characterized by a finite number of bulbs, and a certain partition of the bulbs into "bulb groups". There is thus a one-one correspondence between synapses and neurons. All the bulbs of a synapse will be said to terminate on the neuron associated with the synapse.

Bulb group: A set of bulbs in the same synapse originating at the same neuron. Depending on the number of bulbs in a bulb group, the latter will be referred to as a "single", a "couple", an "n-tuple", etc.

Neural net: The totality of neurons, axones, and synapses considered and their distribution in space.

Synaptic type: Two neurons will be said to be of the same synaptic type if their synapses are characterized by the same number of bulbs and the bulbs are partitioned into bulb groups in the same way.

The following postulates will govern the present formulation. It is the authors' intention to complicate these simple postulates in succeeding formulations so as to approach more plausible representations of actual biological structures.

1. *If a neuron fires, all the terminal bulbs of the axone associated with it are active at the same time.*

This assumption was already stated in the definition of the axone. The postulate supposes instantaneous propagation of impulses along the axones. The same hypothesis governs the McCulloch-Pitts formulation, where it is justified by the fact that for short distances synaptic delay is great compared with the time of propagation along the axone. We will suppose this to hold in the regions considered.

2. *If and only if a number of bulbs at a synapse, not less than the threshold of the associated neuron are active at an instant* t, *the neuron will fire at the instant* $\mathrm{t} + 1$.

This implies a constant "synaptic delay" for all synapses, which is taken as the unit of time. In the present formulation we shall suppose a "state" for a given neural net at the time $t = 0$ and will seek the state of the net for succeeding moments, all integral multiples of our unit.

Certain important concepts which form indispensible features of theories dealing with nervous activity are here deliberately omitted. We have already mentioned that the time of propagation of an impulse along an axone is neglected. Hence the "length" of an axone has no meaning. Distances between neurons, however, will appear in connection with other considerations. The refractory period of a neuron (i.e., the time interval during which it cannot fire, immediately following the time of firing) is likewise omitted from consideration. The omission is justified by our assumptions, if the refractory period is taken smaller than the synaptic delay, since in this case a neuron may fire at two successive moments of our "quantized" time. Finally the omission of inhibitory connections from consideration is conspicuous. These will be included in a future formulation of the problem.

Our neuron, then, is characterized by three variables, namely, the number of bulbs terminating on it, the way these bulbs are partitioned into bulb groups, and its threshold. The first and third of these variables are clearly integers. The second depends on a certain *partition* of an integer.

Let us suppose that six bulbs terminate on the neuron and that they are grouped into two couples and two singles. Then the partition of 6 associated with our synapse is $1 + 1 + 2 + 2$. There are 11 distinct partitions of 6. Hence we may have 11 different kinds of neurons, each having 6 bulbs terminating on it and each having the same threshold. In general if the maximum number of bulbs at any synapse of a neural net is N, and the greatest threshold of any neuron is H, the net may have $Np(N)H$ kinds of neurons, where $p(N)$ is the well known function which gives the number of partitions of an integer.

All the partitions of an integer can be ordered according to some prescribed system. For example, a partition of the integer n can be symbolized by an n-tuple$(i_1, i_2, \cdots i_n)$ of non-negative integers, where i_1 indicates the number of 1's in the partition, i_2, the number of 2's, etc., so that $n = \sum_{s=1}^{n} s i_s$. At least some of the i_s, of course, must be zero. These n-tuples can then be ordered in some prescribed way, for example lexicographically, that is in such a way that the n-tuple $(i_1, i_2, \cdots i_n)$ precedes the n-tuple $(i_1', i_2' \cdots i_n')$ if $i_l > i_l'$ and $i_k = i_k'$ for $k > l$.

If a system of ordering is prescribed for the partitions, the designation of the p-th partition of an integer n is unique. If n denotes the total number of bulbs at a synapse, p the ordinal of the p-th partition of n according to some prescribed system, then n and p determine the synaptic type of the neuron associated with the synapse. If h is the threshold of the neuron, then the three integers n, p, h, completely characterize the neuron. (See Figure 1.)

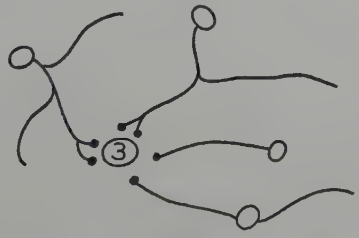

FIGURE 1

It remains to define the parameters which will characterize our neural net.

Probability of synaptic types. The probability that a synapse in an infinitesimal region about the point Q of the region containing the net is of a synaptic type (n, p) will be designated by $S(n, p, Q)$.

Probability of thresholds. The probability that a neuron in an infinitesimal region about Q has threshold h will be denoted by $T(h, Q)$.

Frequency distribution of origins. The probability that a bulb group at Q originates in the infinitesimal region about a point X will be denoted by $O(Q, X)\,dX$.

All three parameters are functions of position Q and other variables. It is to be noted that S and T are actual probabilities. The argument of S besides that of position is a pair of integers; that of T a single integer. The parameter O, however, is a probability frequency distribution. Thus the actual probability that a bulb group at Q originates in a region R' is given by $\int_{R'} O(Q, X)\,dX$. If we suppose that our net is closed, that is every bulb of the net has its origin within the net, we must have $\int_R O(Q, X)\,dX = 1$ for all functions $O(Q, X)$, where the integral is taken over the entire region containing the net.

Let now an initial state of a neural net be given at the time $t = 0$ in the following manner. The function $f_0(X)$ will specify the fraction of neurons in the infinitesimal region dX about X which are firing at the time $t = 0$. The state of the net will be determined for any time t if an expression for $f_t(X)$ is determined. We now seek $f_1(X)$.

Consider a point Q in our region. The probability of firing at $t = 1$ for each neuron in the infinitesimal region about Q depends on the distribution of synaptic types and thresholds around Q and on the frequency distribution of origins at Q. In fact, a neuron at Q will fire at $t = 1$ if a sufficient number of bulbs terminating on it originate at neurons firing at $t = 0$. The probability of a neuron at Q having synaptic type (n, p) is $S(n, p, Q)$, and the probability that its threshold is h is $T(h)$. Therefore, if the two probabilities are independent (as they are supposed to be at this time), the probability of a neuron at Q being determined by the integers n, p, h is $S(n, p, Q)T(h, Q)$.

Now consider the probability that a bulb group of a neuron at Q originates at a neuron firing at $t = 0$. This probability is given by

$$I_0(Q) = \int_R O(Q, X)\, f_0(X)\,dX\,, \tag{1}$$

where the integral is taken over the entire region containing the net.

Consider those neurons for which $p = 1$ in a lexicographic ordering, that is those which have only one bulb group terminating on them. The probability of occurrence of such neurons and of their firing at $t = 1$ will equal $S(n, 1, Q)T(h, Q)I_0$ where $h \leqq n$. But in general, where various combinations of distinct active bulb groups determine the firing of the neuron, the integral I will be replaced by a certain function of I. Let us see what sort of functions come into consideration.

To fix ideas, suppose a neuron at Q has four bulbs terminating on it and threshold 3. Then, if all four bulbs belong to one group, the probability of the neuron firing at $t = 1$ equals the probability that a neuron firing at $t = 0$ sends an axone to the synapse at Q. This probability is I_0. If three of the bulbs are terminals of one axone, the probability is still I_0, since it would be the same as if the synapse contained only three bulbs in one group, because the firing or not firing of the fourth bulb is of no consequence. If, however, the four bulbs are paired off to two axones, both must originate at a neuron firing at $t=0$, and this probability is I_0^2. If the four bulbs are partitioned into two singles and a couple, we must have the couple and at least one of the singles originating at a firing neuron. This probability is $I_0(2I_0 - I_0^2) = 2I_0^2 - I_0^3$. Finally, if all four bulbs are singles, the probability of the neuron at Q firing is the probability that at least three of its four bulbs originate at firing neurons, which is $3I_0^3 - 2I_0^4$.

Thus we see that the probability of Q firing depends on certain polynomials of I. These polynomials depend on n, p, and h and will be designated by $P_{nph}(I)$. Each set of integers (n, p, h) completely determines a polynomial, but different sets may determine the same polynomial.

Neurons associated with the same $P(I)$ will be said to have the same *connectivity type.* Neurons of the same synaptic type are not necessarily of the same connectivity type and vice versa. Neurons having the same (n, p, h) will be said to be of the same *type,* and are, of course, of the same synaptic and the same connectivity type. Thus both synaptic type and threshold determine the connectivity type.

By way of example we exhibit all the polynomials P_{nph} which may arise if $n = 4$. There are five partitions of 4, and we order them as follows:

$p=1$	$p=2$	$p=3$	$p=4$	$p=5$
(0,0,0,1)	(1,0,1,0)	(0,2,0,0)	(2,1,0,0)	(4,0,0,0)

Then

$$\begin{array}{lll}
P_{411} = I & P_{421} = 2I - I^2 & P_{431} = 2I - I^2 \\
P_{412} = I & P_{422} = I & P_{432} = 2I - I^2 \\
P_{413} = I & P_{423} = I & P_{433} = I^2 \\
P_{414} = I & P_{424} = I^2 & P_{434} = I^2
\end{array}$$

$$\begin{aligned} P_{441} &= 3I - 3I^2 + I^3 & P_{451} &= 4I - 6I^2 + 4I^3 - I^4 \\ P_{442} &= I + I^2 - I^3 & P_{452} &= 6I^2 - 9I^3 + 4I^4 \\ P_{443} &= 2I^2 - I^3 & P_{453} &= 3I^3 - 2I^4 \\ P_{444} &= I^3 & P_{454} &= I^4 \end{aligned}$$

Since the types of neurons characterized by distinct sets (n, p, h) are mutually exclusive, the probability of a neuron at Q firing at the time $t = 1$ will be given by the sum of the probabilities of its being of each type and firing.

Now we assume that the number of neurons in the region at Q is large compared with the number of bulb groups originating at the same neuron. This assumption enables us to say that the fraction of neurons firing in the region about Q at $t = 1$ equals the probability of a neuron in that region firing at $t = 1$.

We can now give an analytic expression for $f_1(Q)$ in terms of $f_0(Q)$ and the parameters of the net:

$$f_1(Q) = \sum_{n=1}^{n=\infty} \sum_{p=1}^{p=p(n)} S(n, p, Q) \sum_{h=1}^{h=n} T(h, Q) P_{nph}[I_0(Q)], \tag{2}$$

where

$$I_0(Q) = \int_R f_0(X) O(Q, X) dX .$$

III.

In what follows we shall illustrate some implications of equation (2) by applying it to some very simple cases.

Case 1: *Constant initial firing distribution; constant threshold; equiprobability of* n; p $= 1$.

Consider a neural net with the following properties.

1. The number of bulbs terminating on any neuron does not exceed N.
2. The number of bulb groups at any synapse does not exceed one.
3. All the synaptic types $\{n, 1\}$, where $n = 1 \cdots N$, are equally probable.
4. The threshold of every neuron is h^*, a constant.
5. The initial state of the net $f_0(X) = f_0$, a constant throughout the region.

By the above assumptions we have

$$S(n, 1, Q) = 1/N; \quad S(n, p, Q) = 0 \text{ for } p \neq 1, \tag{3}$$

$$T(h;Q)=\delta_{h^*h}, \tag{4}$$

$$I_0=\int_R f_0 O(Q,X)\,dX=f_0. \tag{5}$$

Thus equation (2) reduces to

$$f_1(Q)=\sum_{n=1}^{n=N}(1/N)\sum_{h=1}^{h=n}\delta_{h^*h}\,f_0=\frac{N-h^*+1}{N}f_0. \tag{6}$$

Since the process is reiterative, we obtain

$$f_t=\frac{N-h^*+1}{N}f_{t-1}. \tag{7}$$

And by induction

$$f_t=\left(\frac{N-h^*+1}{N}\right)^t f_0. \tag{8}$$

Obviously f_t will be independent of t if and only if $h^*=1$. Otherwise f_t will tend to zero as a geometric sequence with the ratio $(N-h^*+1)/N$. In this case the ratio is independent of f_t. We shall give examples below where it does depend on f_t. In all cases we shall refer to the ratio f_{t+1}/f_t as the *firing ratio* (in general a function of f_t). If the firing ratio is always less than unity, we shall refer to it as the *decay factor.*

Case 2. *Equiprobability of* n *and* h. *Threshold of any neuron does not exceed* H.

If we suppose the same net as in Case 1, except that the thresholds are randomly distributed, we obtain after similar computation the firing ratio for this net, which turns out to be also a decay factor independent of f_t, namely,

$$f_{t+1}/f_t=\left(\frac{2N+1-H}{2N}\right)f_t. \tag{9}$$

Thus

$$f_t=\left(\frac{2N+1-H}{2N}\right)^t f_0,\ \text{independent of } t \text{ if } H=1.$$

The decay factors in Cases 1 and 2 are equal if $h=(N+1)/2$, which is intuitively evident.

Case 3. *Bernoulli Distribution of Thresholds*; *equiprobability of* n; $n_{\max}=h_{\max}=N$.

We have in this case

$$T(h) = \frac{1}{2^{N-1}} \binom{N-1}{k-1}, \tag{10}$$

$$\sum_{k=1}^{n} T(h) = \frac{1}{2^{N-1}} \sum_{r=0}^{n-1} (n-r) \binom{N-1}{r},$$

which gives for the decay factor

$$f_{t+1}/f_t = \frac{1}{N2^{N-1}} \sum_{n=1}^{n=N} \sum_{r=0}^{r=n-1} (n-r) \binom{N-1}{r}. \tag{11}$$

This can be expressed as a single sum as follows:

$$f_{t+1}/f_t = \frac{1}{N2^{N-1}} \sum_{r=0}^{r=n-1} (N-r) \binom{N-1}{r}. \tag{12}$$

Case 4. *Equiprobability of* h; *Bernoulli distribution of* n. In this case

$$T(h) = 1/N, \tag{13}$$

$$S(n) = \frac{1}{2^{N-1}} \binom{N-1}{n-1}, \tag{14}$$

and the decay factor is given by

$$\sum_{n=1}^{n=N} \frac{1}{N2^{N-1}} \binom{N-1}{n-1} \sum_{k=1}^{k=n} 1/N = \sum_{n=1}^{n=N} \frac{1}{N2^{N-1}}\, n \binom{N-1}{n-1}. \tag{15}$$

By symmetry of binomial coefficients it follows that

$$\sum_{n=1}^{n=N} n \binom{N-1}{n-1} = \sum_{r=0}^{r=N-1} (N-r) \binom{N-1}{r}, \tag{16}$$

so that the decay factors in Cases 3 and 4 are identical.

Case 5. *Bernoulli Distribution for both* n *and* h.

This case yields the decay factor

$$\frac{1}{2^{2N-2}} \sum_{n=1}^{n=N} \binom{N-1}{n-1} \sum_{h=1}^{h=n} \binom{N-1}{h-1} = \frac{1}{2^{2N-2}} \left\{ 1 + \left[1 + \binom{N-1}{1} \right] \binom{N-1}{1} + \left[1 + \binom{N-1}{1} + \binom{N-2}{2} \right] \binom{N-2}{2} + \cdots \right\}. \tag{17}$$

Case 6. *Connectivity Types Determined by Two Equal or Nearly Equal Bulb Groups at Every Synapse.*

Consider a neural net in which every synapse contains exactly two bulb groups with either equally distributed bulbs (if n is even) or differing by one bulb (if n is odd). Let also all thresholds and bulb numbers be equiprobable. The maximum number of bulbs occurring, N, will be taken as an even integer for simplicity (the arguments for an odd integer are very similar). Then all the neurons of the net which can fire at all are divided into the following connectivity types.

1. Where the activity of either group is sufficient to fire the neuron. Here $P(I) = 2I - I^2$.
2. Where the activity of the larger group is necessary and sufficient to fire the neuron. Here $P(I) = I$.
3. Where the activity of both groups is necessary to fire the neuron. Here $P(I) = I^2$.

To the first connectivity type belong those neurons in which $h < \frac{1}{2}(n + 1)$. To the second belong those where $h = \frac{1}{2}(n + 1)$. To the third belong the neurons characterized by $N \geqq k > \frac{1}{2}(n + 1)$. Here for a constant initial distribution we obtain

$$f_{t+1}\left[\sum_{n=1}^{n=N/2} S(2n) \sum_{h=1}^{h=n} T(h) + \sum_{n=1}^{n=N/2-1} S(2n+1) \sum_{h=1}^{h=n} T(h)\right](2I_t - I_t^2)$$

$$+\left[\sum_{n=1}^{n=N/2} S(2n-1)\,T(n)\right] I_t + \left[\sum_{n=1}^{n=N/2} S(2n) \sum_{h=n+1}^{h=2n} T(h)\right. \tag{18}$$

$$\left. + \sum_{n=1}^{n=N/2-1} S(2n+1) \sum_{h=n+1}^{h=2n} T(h)\right] I_t^2 .$$

Since $I_t = f_t$, we obtain for the firing ratio after laborious but elementary calculations

$$f_{t+1}/f_t = \frac{4N + f_t(N-2)}{8N}. \tag{19}$$

Since $f_0 \leqq 1$, the firing ratio is always less than unity and again $\lim_{t\to\infty} f_t = 0$.

IV.

The presence of the decay factor in Cases 1–6 is due to the fact that our neural nets contained neurons which can *never* fire, i.e., those whose thresholds exceed their bulb numbers. The proportion of such neurons is determined by the distributions of synaptic types and thresholds. It turned out in the cases considered that the proportion of "non-functional" neurons was so high that decay factors were always present. We are interested in determining conditions under which there would be no decay factor, i.e., we wish the firing ratio $f_{t+1}/f_t \geqq 1$. To simplify the problem we shall prescribe not distributions of synaptic types and thresholds but a distribution of *connectivity types.* It will be shown in the case under consideration that this distribution determines the firing ratios.

We wish every neuron to be characterized by a connectivity type. Therefore, we will assign to non-functional neurons the connectivity type 0 (i.e., the polynomials $P(I)$ associated with them are identically zero). If λ_{nph} represents the fraction of neurons in the net of type (n, p, h) we have $\sum_{n,p,h} \lambda_{nph} = 1$. Furthermore, we can write equation (2) in a simpler form, namely

$$f_1 = \sum_{n,p,h} \lambda_{nph} P_{nph}(I_0), \tag{20}$$

where some P_{nph} may be zero.

In the cases considered above the quantities λ_{nph} were not prescribed in advance but were computed from the probability distributions of synaptic types and thresholds. We wish now to consider the relation between the distribution of *connectivity types* and the overall behavior of the net. For this reason, instead of prescribing the distributions of synaptic types and thresholds, we shall prescribe the distribution of connectivity types for our neural net.

Case 7. *Prescribed Distribution of Connectivity Types.*

Let λ_0, λ_1, λ_2, λ_3 be the respective fractions of neurons having connectivities 0, I, I^2 and $2I - I^2$ respectively. Let there be no other connectivity types and suppose as previously a constant initial firing distribution f_0. We have obviously

$$\sum_{i=0}^{i=3} \lambda_i = 1. \tag{21}$$

Let us put $\lambda_1 + \lambda_2 + \lambda_3 = \lambda$.
Since $I_0 = f_0$, we have

$$\begin{aligned} f_1 &= \lambda_1 f_0 + \lambda_2 f_0^2 + \lambda_3 (2f_0 - f_0^2), \\ &= f_0(\lambda_1 + 2\lambda_3) + f_0^2(\lambda_2 - \lambda_3); \end{aligned} \tag{22}$$

and in general

$$f_{t+1} = f_t(\lambda_1 + 2\lambda_3) + f_t^2(\lambda_2 - \lambda_3). \tag{23}$$

The firing ratio is given by

$$f_{t+1}/f_t = \lambda_1 + 2\lambda_3 + f_t(\lambda_2 - \lambda_3). \tag{24}$$

Let $\lambda_3 > \lambda_2$. Then the firing ratio will exceed unity if

$$\lambda_1 + 2\lambda_3 > 1 - f_t(\lambda_2 - \lambda_3) = 1 + f_t(\lambda_3 - \lambda_2); \tag{25}$$

$$f_t < \frac{\lambda_1 + 2\lambda_3 - 1}{\lambda_3 - \lambda_2}. \tag{26}$$

Substituting the value of λ_3 from equation (21) into (26), we obtain as a condition for a firing ratio greater than unity

$$f_t < \frac{2\lambda - \lambda_1 - 2\lambda_2 - 1}{\lambda - 2\lambda_2 - \lambda_1} = 1 - \frac{1 - \lambda}{\lambda - 2\lambda_2 - \lambda_1}. \tag{27}$$

Note that since $\lambda_3 > \lambda_2$, $\lambda > 2\lambda_2 + \lambda_1$. Also $1 \geqq \lambda$.

Hence $\dfrac{1-\lambda}{\lambda - 2\lambda_2 - \lambda_1} > 0$. If now $1 - \lambda < \lambda - 2\lambda_2 - \lambda_1$, condition (27) is possible to satisfy. This implies that $1 < 2\lambda_3 + \lambda_1$, which is a stronger condition than $\lambda_3 > \lambda_2$.

A similar argument shows that the firing ratio will be less than unity provided $\lambda_3 > \lambda_2$ and $1 > 2\lambda_3 + \lambda_1$. Suppose now $\lambda_2 > \lambda_3$. Then in equality (25) reduces to

$$f_t > \frac{1 - 2\lambda_3 - \lambda_1}{\lambda_2 - \lambda_3} = \frac{1 - 2\lambda + \lambda_1 + 2\lambda_2}{2\lambda_2 + \lambda_1 - \lambda}, \tag{28}$$

$$f_t > 1 + \frac{1 - \lambda}{2\lambda_2 + \lambda_1 - \lambda} > 1, \tag{29}$$

which is impossible. We have thus deduced the conditions on f_t and on the distributions of connectivity types for the case considered such that the firing ratio is greater or less than unity. They are summarized as follows:

A necessary and sufficient condition under Case 7 for the firing ratio to exceed unity is

$$1 < 2\lambda_3 + \lambda_1 ; f_t < 1 - \frac{1 - \lambda}{\lambda - 2\lambda_2 - \lambda_1}. \tag{30}$$

In particular if $\lambda = 1$, $\lambda_3 > \lambda_2$ we have $\lim_{t \to \infty} f_t = 1$, that is eventually every neuron in the net will be firing.

V.

The examples considered here were especially simple because of the triviality of the initial firing distribution (a constant throughout the region) and of the synaptic types and thresholds (likewise constant throughout the region). This situation yields the simple relation $I_t = f_t$, which allows the calculation of successive states by simple iteration. If, however, $f_0(X)$ is a non-trivial function of position, or the neuron types are distributed non-uniformly, the problem is considerably complicated. The general expression for $f_1(Q)$ is given by equation (2) or equation (20). In the latter equation the coefficients of P_{mph} are certain quantities $\lambda_{nph}(Q)$ which represent the fractions of the totality of neurons which are characterized by the connectivity type polynomials $P_{nph}[I(Q)]$. These fractions can be in principle computed from the distributions of the synaptic types and thresholds. If they are assumed as known, equation (2) takes the form

$$f_1(Q) = \sum_{n,p,h} \lambda_{nph}(Q) P_{nph}\left[\, I_0(Q) \,\right] \tag{31}$$

where in general $I_0(Q)$ is a function of Q.

A question of fundamental interest is the possibility of existence of a steady state of neural activity, given the parameters of the net and an initial firing distribution.

Such a steady state, constant with respect to time(if it exists) will be given by the solution of the integral equation

$$f_t(Q) = \sum_{n,p,h} \lambda_{nph}(Q) P_{nph}\left[\int_R f_t(X) O(Q, X)\, dX \right] \tag{32}$$

since the equation implies that $f_{t+1} = f_t$.

In general the equation is non linear, since the polynomials P_{nph} are in general of degree greater than one.

The equation reduces to a linear one if all connectivities are of the type $P_{nph}(I) = I$, which implies that the firing of each neuron is determined by the activity of a single bulb group.

The solution of equation (32) establishes only the possibility of a steady state. Questions of convergence toward such a state from a given initial distribution must be separately considered.

The authors are indebted to Dr. L. J. Savage for a critical discussion of this paper.

This work was aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.

LITERATURE

Lashley, K. S. 1926. "Studies of Cerebral Function in Learning. VII. 'The Relation Between Cerebral Mass, Learning and Retention.' " *J. Comp. Neurol.*, 41, 1–58.

McCulloch, W. S., and Pitts, W. 1943. "A Logical Calculus of the Ideas Immanent in Nervous Activity." *Bull. Math. Biophysics*, 5, 115–133.

McCulloch, W. S., and Pitts, W. 1947. "How We Know Universals. The Perception of Auditory and Visual Forms." *Bull. Math. Biophysics,* 9, 127–147.

Newman, H. H. 1940. *Multiple Human Births.* New York: Doubleday, Doran & Co., Inc.